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VEGETATIVE STRUCTURES OF THE CALLISTOPHYTACEAE
(PTERIDOSPERMOPSIDA)

by

© GAR WILLIAM ROTHWELL

A THESIS
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IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Vegetative Structures of the Callistophytaceae (Pteridospermopsida)." submitted by Gar William Rothwell in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The discovery of numerous Upper Pennsylvanian age specimens of *Callistophyton poroxyloides* and abundant material of a previously unrecognized Middle Pennsylvanian age *Callistophyton* provides the basis for an examination of the vegetative features of the Callistophytaceae. The structure and anatomy of the stems, buds, branches and leaves are elaborated, and roots are described for the first time. Emphasis is placed on the specific identity of material from different stratigraphic and geographic locations, and developmental features of the plant organs are interpreted. Material previously described as *Poroxylon boyssetii*, *Poroxylon edwardsii* and *Calamopitys kansanum* is reexamined and found to be specifically equivalent to the Middle Pennsylvanian *Callistophyton*. Amended diagnoses are provided for the genus *Callistophyton*, for *C. poroxyloides*, and for the new combination, *C. boyssetii*. The relationships of the Callistophytaceae are interpreted in relation to both vegetative and fertile structures of the family, and implications to the currently recognized phylogeny of gymnosperms are discussed. A reconstruction of *Callistophyton* is also included.

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INTRODUCTION

Callistophyton poroxyloides Delevoryas and Morgan (1954) is one of the most recently discovered of Pennsylvanian age pteridosperms. Nevertheless, it is represented by both vegetative and fertile parts and is rapidly emerging as one of the best known Paleozoic plants. Since the original description of the stems, buds and leaves (Delevoryas and Morgan, 1954) our knowledge of the plant has been augmented by the discovery of a well-preserved stem apex with immature leaves (Delevoryas, 1956), and by the description of pollen organs attached to the fronds (Stidd and Hall, 1970a). On the basis of association and anatomical similarity, ovules have also been assigned to *C. poroxyloides* (Stidd and Hall, 1970b). These combined plant parts are now recognized as the Callistophytaceae (Stidd and Hall, 1970b), a distinct family of pteridosperms from the Upper Pennsylvanian of Illinois. Plant organs assignable to *C. poroxyloides* include stems, buds and fern-like leaves. Roots have not been reported. The pollen organs are described as *Callandrium callistophytoides* Stidd and Hall (1970b), while the ovules are referred to as *Callospermarion pusillum* Eggert and Delevoryas (1960)Stidd and Hall (1970b).

More recently, a Middle Pennsylvanian pollen organ from Illinois has also been assigned to the Callistophytaceae (Rothwell, 1972b), and indicates the presence of the family in these somewhat older strata. In addition, *Callistophyton* type stems have been reported from the Middle Pennsylvanian of Kansas (Baxter and Hornbaker, 1965) and Illinois (Millay and Eggert, 1970; Rothwell, 1972a), and *Callospermarion* type ovules have been reported from the Middle Pennsylvanian of Illinois (Rothwell, 1972a).

The Present Study

The current investigation was undertaken to increase our knowledge of the Upper Pennsylvanian age *Callistophyton poroxyloides*, and to describe new Middle Pennsylvanian specimens. The study deals with morphological and anatomical features of the vegetative *Callistophyton* plant parts that are present in North American coal balls. An additional aspect of the investigation is the detailed comparison of *Callistophyton* material to 1) presumably cordaitean material described as *Poroxylon boyssetii* Renault (1879b) and *P. edwardsii* Renault (1880), and 2) to a Middle Pennsylvanian pteridospermous stem fragment from Kansas described as *Calamopitys kansanum* Baxter and Roth (1953). The critera used for taxonomic interpretation include plant habit, structure of the vegetative organs and anatomical features. Primary vasculature is also used as a criterion for determining the relationships of these plants. Special emphasis is placed on the specific identity of the specimens found at differing geographic locations and stratigraphic levels, and developmental features are discussed whenever sufficient well-preserved material is available for interpretation.

Based on the structure and development of the stems, leaves, buds, branches, and roots, two distinct species of *Callistophyton* can be identified in North American coal-ball material of Pennsylvanian age. *Callistophyton* *poroxyloides* occurs in Upper Pennsylvanian sediments from Illinois. A second species not previously assigned to *Callistophyton* occurs in Middle Pennsylvanian material from Illinois, Kentucky and Kansas. In addition, the material described as *Poroxylon boyssetii*, *P. edwardsii*, and *Calamopitys kansanum* is interpreted as being specifically equivalent to the Middle Pennsylvanian *Callistophyton* species. Features that distinguish the Upper Pennsylvanian *Callistophyton poroxyloides* from the Middle Pennsylvanian species include the development of the primary wood, the structure of cortical appendages, and numerous other anatomical features.

Collecting Localities and Stratigraphy

The material investigated in this study was collected at eight coal-ball (carbonate petrifaction) localities in North America, and one silicified petrifaction locality in France. Of these, the Sahara and Berryville localities in Illinois have provided the largest number of specimens.

Localities

Autun	Unspecified location near Autun (46.57N, 4.18E), France.
Berryville	SW¼, NE¼, NW¼, Sec. 7, T. 2 N., R. 13 W, Sumner Quadrangle, Lawrence County, Illinois. 6 miles south and 2 miles west of Sumner, Illinois, U.S.A..
Calhoun	Sec. 32, T. 3 N., R. 14 W., Sumner Quadrangle, Richland County. 2.6 miles east of Calhoun, Illinois, U.S.A..
Dix	Sec. 20, T. 1 S., R. 3 E., Mount Vernon Quadrangle, Jefferson County. 3 miles southeast of Dix, Illinois, U.S.A..
New Calhoun	Sec. 32, T. 3 N., R. 14 W., Sumner Quadrangle, Richland County. 2.6 miles east of Calhoun, Illinois, U.S.A..
Pit #11	Sec. 5, T. 31 N., R. 9 E., Herscher Quadrangle, Kankakee County. 2 miles NW of Essex, Illinois, U.S.A..

Providence	NE¼, Providence Quadrangle by Kentucky topographic map co-ordinate system x 412,200' y 407,700'. 1½ miles NW of the center of the town of Providence, Kentucky, U.S.A..
Sahara	Sec. 30, T. 9 S., R. 4 E., Harrisburg Quadrangle, Williamson County. 4 miles northwest of Carrier Mills, Illinois, U.S.A..
West Mineral	W. ¼, Sec. 5, T. 33 S., R. 22 E. Columbus Quadrangle, Cherokee County, Kansas, U.S.A..

Stratigraphic Position and Age

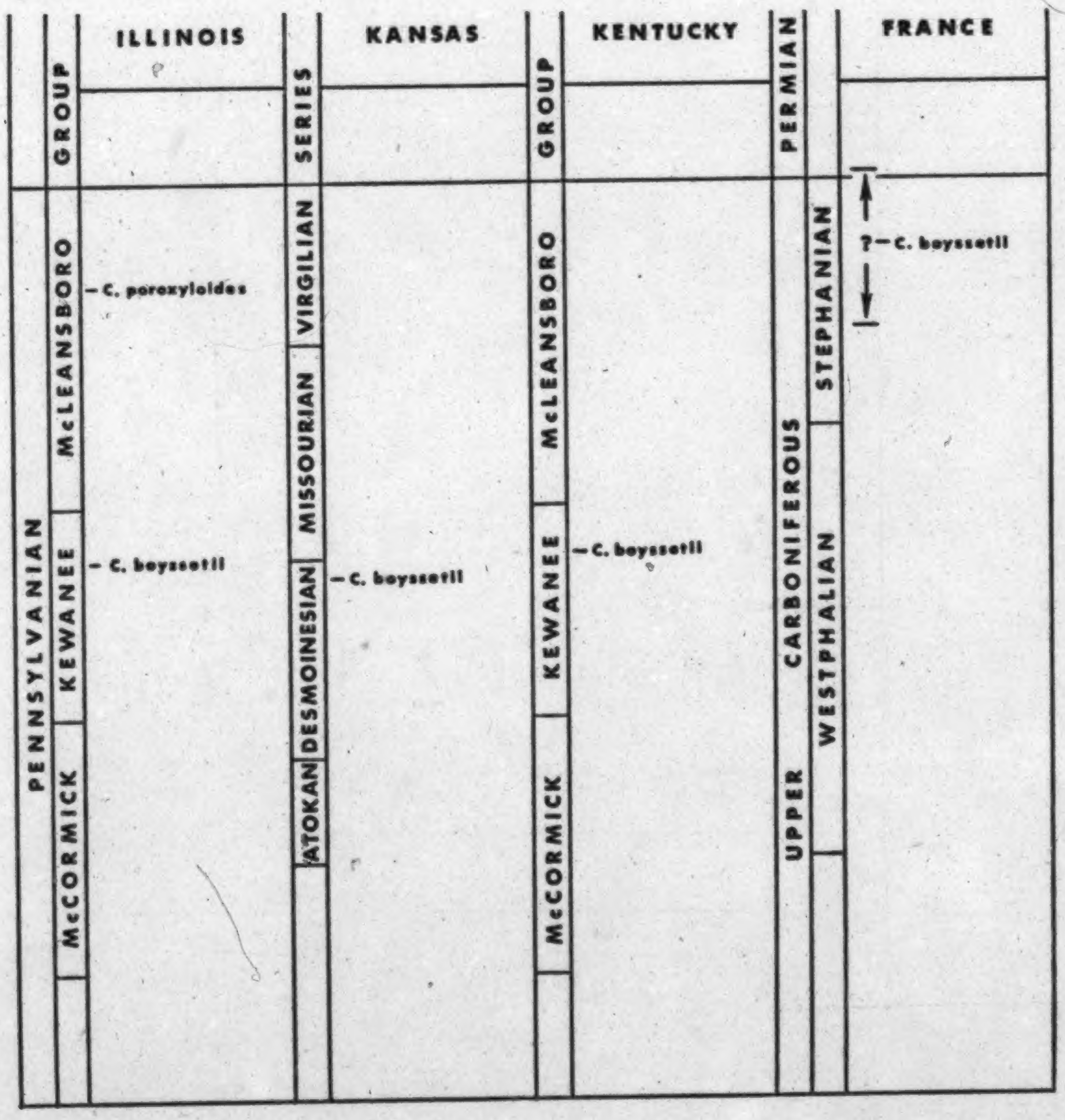
Autun	Unspecified coal from the Autun Basin. See explanation below.
Berryville	Calhoun Coal, Mattoon Formation, McLeansboro Group. Upper Pennsylvanian (Illinois)
Calhoun	Calhoun Coal, Mattoon Formation, McLeansboro Group. Upper Pennsylvanian (Illinois)
Dix	Calhoun Coal?, Mattoon Formation, McLeansboro Group. Upper Pennsylvanian (Illinois)
New Calhoun	Calhoun Coal, Mattoon Formation, McLeansboro Group. Upper Pennsylvanian (Illinois)

Pit #11	Colchester (No. 2) Coal, Carbondale Group, Kewanee Formation. Middle Pennsylvanian (Illinois)
Providence	Coal No. 12, Carbondale Fo-mation, Kewanee Group. Middle Pennsylvanian (Kentucky)
Sahara	Herrin No. 6 Coal, Carbondale Formation, Kewanee Group. Middle Pennsylvanian (Illinois)
West Mineral	Fleming Coal, Cabaniss Subgroup, Cherokee Group, Desmoinesian Series. Middle Pennsylvanian (Kansas)

Notes Concerning Stratigraphic Placement

The four localities that provide specimens of *Callistophyton poroxyloides* are located within a relatively short distance of one another in southeastern Illinois. Specimens from these localities are all collected from the same coal seam. On the basis of present information, one must consider this species to be quite restricted in both geographic and stratigraphic ranges. The Middle Pennsylvanian *Callistophyton* species appears to have a much wider geographic distribution. This latter species has been collected from the eastern Interior- (Illinois, Kentucky) and Mid Continent- (Kansas) Basins of North America, and the Autun Basin of France. Stratigraphically, specimens of the Middle Pensylvanian species occur at relatively equivalent levels in North America (Table 1). The specimens from

TABLE 1. Stratigraphic and geographic distribution of *Callistophyton*.
(Modified after Taylor, 1965).


ILLINOIS
KANSAS
KENTUCKY
FRANCE
GROUP
SERIES
GROUP
PERMIAN
PENNSYLVANIAN
McLEANSBORO
— C. poroxyloides
KEWANEE
— C. boyssetii
McCORMICK
VIRGILIAN
MISSOURIAN
DESMOINESIAN
— C. boyssetii
ATOKAN
McLEANSBORO
KEWANEE
— C. boyssetii
McCORMICK
UPPER CARBONIFEROUS
STEPHANIAN
?— C. boyssetii
WESTPHALIAN

France, however, may be from more recent strata.

As originally interpreted, the Autun specimens of *Callistophyton* (= *Poroxylon boyssetii* and *P. edwardsii* of Renault, 1879b, 1880) were from Permian deposits. Unfortunately, the Upper Carboniferous-Permian boundary is often difficult to identify in this region, and early stratigraphic interpretations are not always reliable. In the present instance, the problem is further complicated by the absence of specific data concerning either the geographic location or coal seam where the specimens were collected. The original descriptions merely indicate that the material was preserved in silicified nodules collected from a coal seam near Autun (Renault, 1879b; Bertrand and Renault, 1886b). The stratigraphy of the region surrounding Autun has been more recently interpreted by Louis (1954), who indicates that the town is situated at the southern edge, near the western margin of the Autun Basin. Sediments in the basin are interpreted as ranging from Stephanian (Upper Carboniferous) to Triassic in age. There are several coal seams within the Stephanian-Permian strata. Of the three presumably Stephanian coal bearing zones, the central zone ("Étage moyen du Mont Pele" of Louis, 1954) is known to occur in the area of Autun. This coal is the most probable source of the Autun material. The lowermost of the Permian strata ("L étage d'Igornay-Lally" of Louis, 1954) closely resembles the Stephanian deposits. Lower Permian coals occur at the western margin of the basin and therefore could possibly also be the source of the Autun specimens. The situation is further complicated by the possibility that all but the lowermost coal beds of the Autun Basin may represent Permian or younger deposits (Louis, 1954). This interpretation is based on the presence of a presumably Permian species of compression fern-like foliage, *Pecopteris pluckeneti*, in the upper two "Stephanian" zones ("Étage moyen du Mont Pele", and the "Faisceau houiller Superior de C. Mollay", Louis, 1954).

In the absence of precise data regarding the ages of the various strata of the Autun Basin and the source of the specimens, the age of the material from Autun can be interpreted as being as old as mid-Stephanian, or as young as lowermost Permian. If one considers the specimens to be of the former age, then they are somewhat younger than the equivalent material from North America, and older than specimens of *Callistophyton poroxyloides*. If, on the other hand, they are interpreted as being of Permian age, then they are younger than the North American material of either species.

Directory of Specimens

The material investigated in this study consists of a large number of coal balls, peel preparations and microscope slides that are housed in several different collections. These are #45-54, 2,986-3,321, #11,963-11,976 in the Paleobotanical Collections, Department of Botany, Ohio University, Athens, Ohio; #5,932-6,477, #11,865-11,916 in the Paleobotanical Collection, Department of Biological Sciences, University of Illinois at Chicago Circle, Chicago, Illinois; #2,227-2,265 in the Paleobotanical Collection, Department of Botany, University of Alberta, Edmonton, Canada; #132-1 - 132-10 in the Paleobotanical Collection, Department of Botany, University of Texas, Austin, Texas; #272-283, #1,388-1,420, #2,224 in the Paleobotanical Collections, Botany Department (Morrill Hall), University of Illinois, Urbana, Illinois; #1,454-1,432, #1,630, #2,964-2,965, #3,279-3,293, #3,332-3,346, #3,386, #3,390-3,391 in the Department of Palaeontology, British Museum (Natural History); #1,454 in the Paleobotanical Collection of R.W. Baxter, Botany Department, University of Kansas, Lawrence, Kansas. Those specimens that are figured in the illustrations and line diagrams, or discussed in the text are identified below by a three part letter and number designation. The first part of the designation refers to the species. The letters CP are used for specimens of *Callistophyton poroxyloides*, and CB is used for specimens of the second species described in this study. The second part of the designation refers to the collecting locality of the specimen.

Designations for the localities are as follows: A = Autun, B - Berryville, D = Dix, P = Pit #11, S = Sahara, and W = West Mineral. The number designations for specimens of each species are arbitrary. The coal-ball number or collection number, and repository are indicated for each specimen below.

Specimen	
CP-B-1	Coal ball 1,221. University of Illinois, Urbana Coal ball 5,821. Ohio University
CP-B-2	Coal ball 1,221. University of Illinois, Urbana Coal ball 5,821. Ohio University
CP-B-3	Coal ball 5,821. Ohio University
CP-B-4	Coal ball 5,821. Ohio University
CP-D-5	Coal ball 132. University of Texasois, Urbana
CP-B-6	Coal ball 1,160. University of Illinois, Urbana
CP-B-7	Collection #2,224. University of Illinois, Urbana
CP-B-8	Coal ball 3,791. University of Illinois, Chicago Circle
CP-B-9	Coal ball 5,821. Ohio University
CP-B-10	Coal ball 5,821. Ohio University
CP-B-11	Coal ball 4,127. University of Illinois,

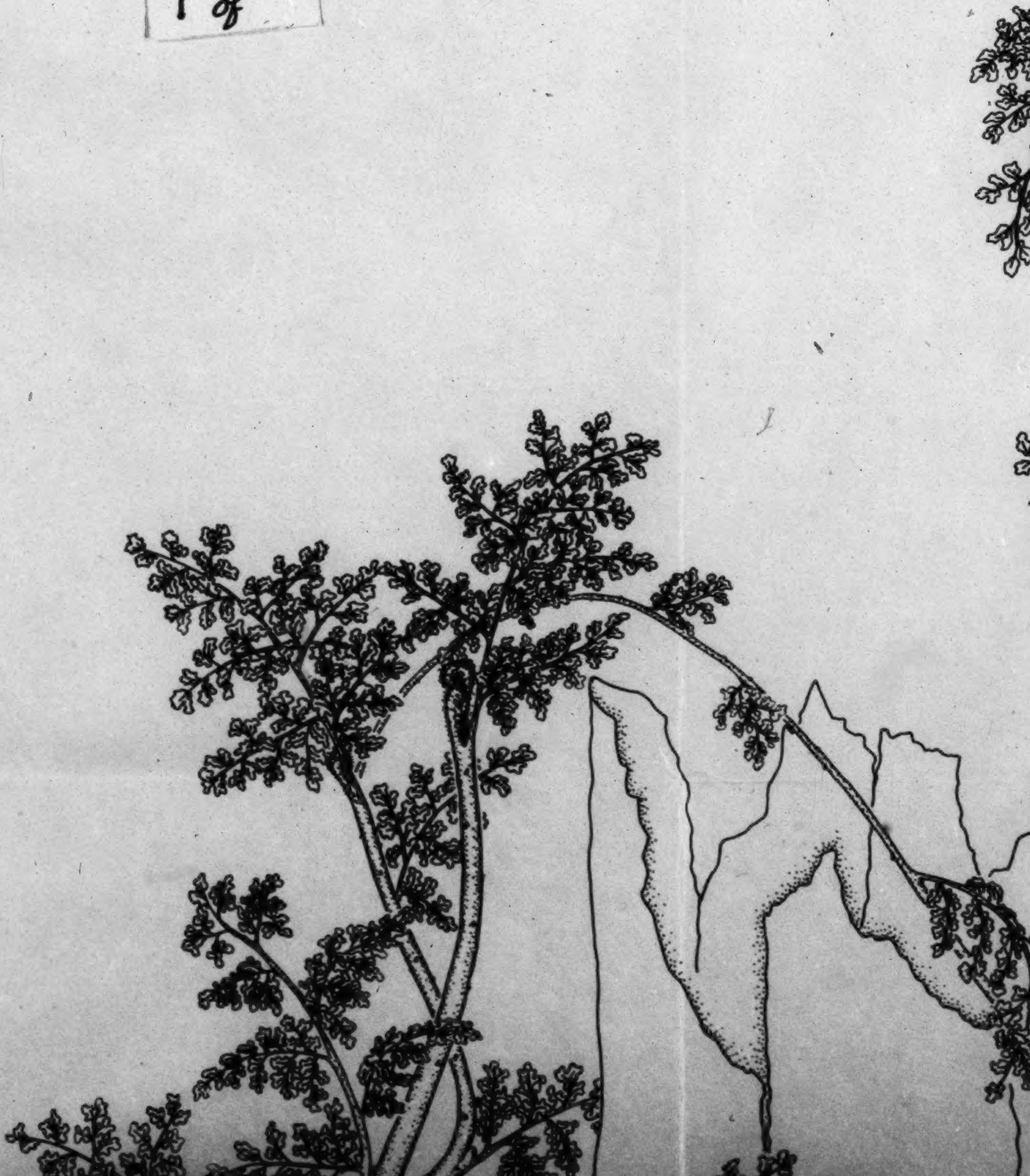
Chicago Circle

CB-S-1	Coal ball 3,259. University of Illinois, Chicago Circle.
CB-S-2	Coal ball 5,754. Ohio University
CB-S-3	Coal ball 289. University of Alberta.
CB-W-4	Collection #1,454. University of Kansas.
CB-A-5	Collection #1,430 British Museum 1,431 British Museum 1,636. British Museum
CB-A-6	Collection #1,428. British Museum
CB-A-7	Collection #2,964. British Museum
CB-S-8	Coal ball 4,007. University of Illinois, Chicago Circle.
CB-S-9	Coal ball 3,521. University of Illinois, Chicago Circle.
CB-S-10	Coal ball 3,521. University of Illinois, Chicago Circle.
CB-S-11	Coal ball 5,754. Ohio University
CB-A-12	Collection #1,421. British Museum
CB-S-13	Coal ball 3,987. University of Illinois, Chicago Circle.
CB-S-14	Coal ball 4,040. University of Illinois, Chicago Circle.
CB-S-15	Coal ball 3,554. University of Illinois, Chicago Circle.
CB-S-16	Coal ball 4,123. University of Illinois, Chicago Circle.

CB-A-17	Collection #2,965. British Museum
CB-A-18	Collection #1,432. British Museum
CB-A-19	Collection #1,423. British Museum
CB-S-20	Coal ball 908. Ohio University
CB-S-21	Coal ball 3,963. University of Illinois, Chicago Circle.
CB-S-22	Coal ball 908. Ohio University
CB-S-23	Coal ball 908. Ohio University
CB-S-24	Coal ball 4,127. University of Illinois, Chicago Circle.
CB-S-25	Coal ball 5,754. Ohio University
CB-S-26	Coal ball 5,754. Ohio University
CB-S-27	Coal ball 327. Ohio University
CB-S-28	Coal ball 2,380. Ohio University
CB-S-29	Coal ball 289. University of Alberta
CB-S-30	Coal ball 5,754. Ohio University
CB-S-31	Coal ball 908. Ohio University

Text Fig. 1. Reconstruction of *Callistophyton*. The plant is illustrated as a small, somewhat scrambling shrub, that is growing on the coal swamp floor near the stump of a dead tree. The reconstruction is based on the specimens that are specifically designated under "plant habit" in the text. X ½

1 of



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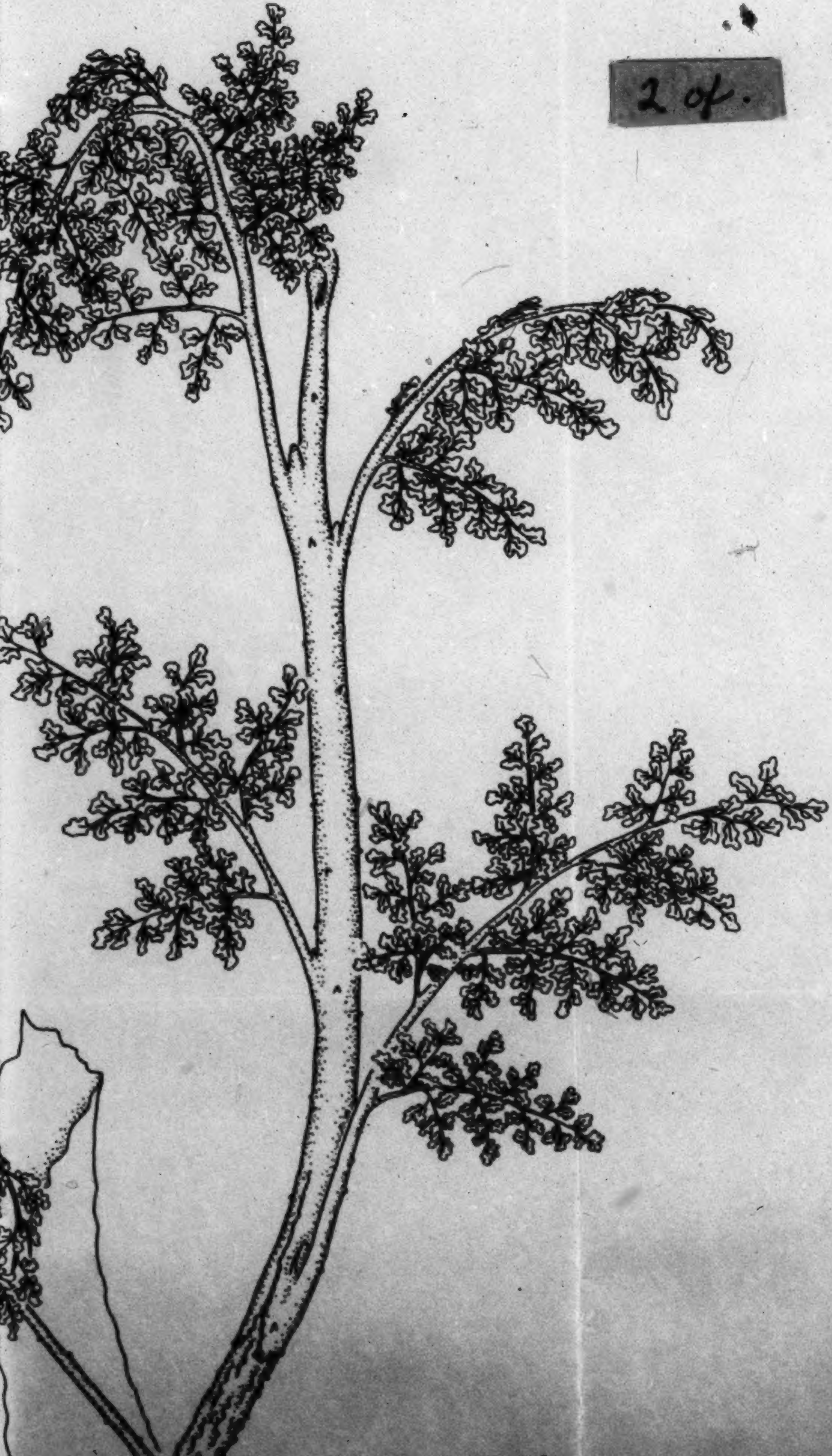

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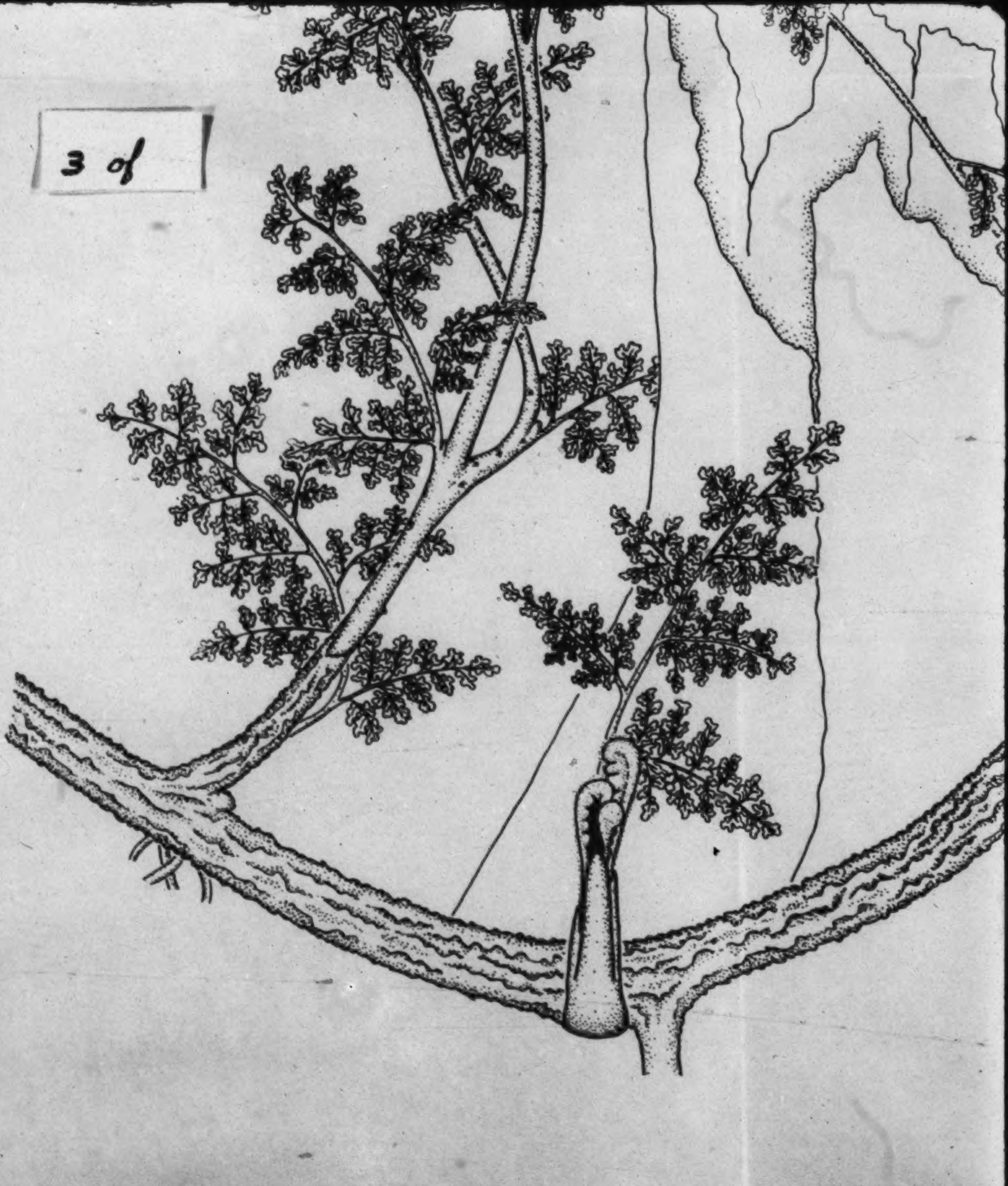

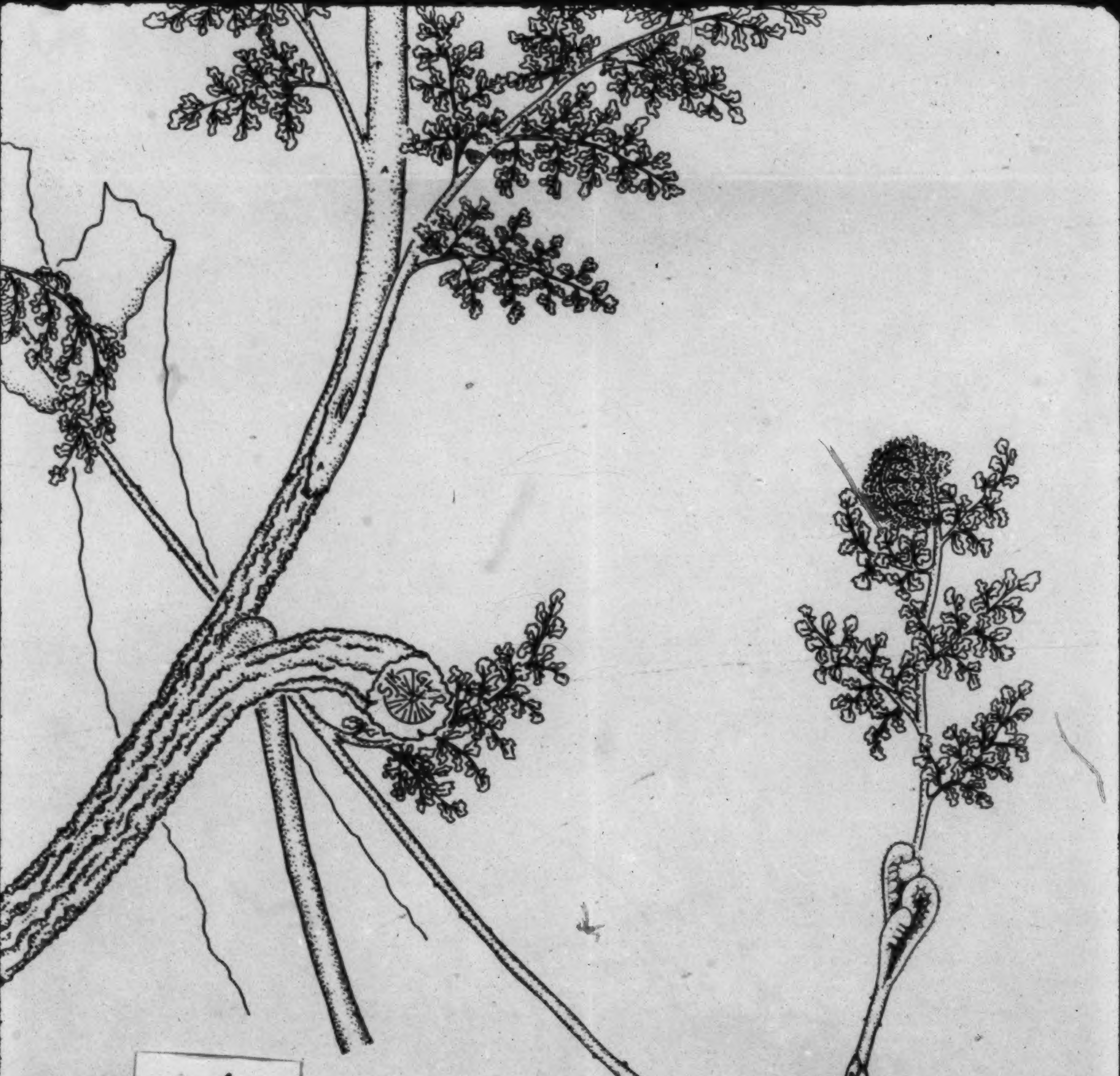

4 of 4

DESCRIPTION OF MATERIAL

General Features

Callistophyton specimens occur as fragments of stems, leaves, buds, branches and roots. Fragments are most often isolated, but the occasional attachment of the various parts to one another demonstrates their identity as organs of the same type of plant. Isolated fragments can be identified by their structural similarity to attached specimens and by several distinctive anatomical features. *Callistophyton* stems are radially symmetrical and slender, measuring 0.2 - 3.0 cm in diameter (Fig. 19-23, 28-33). Leaves are borne at slightly swollen nodes, and at intervals that range from less than one mm, to over 20 cm. The leaves are typically pinnately compound and fern-like, but there is considerable variation in both leaf size and complexity. The largest leaves probably measure as much as 30 cm long and are tri- or quadripinnately compound. Those leaves that are borne on the smaller stems are often less than 5 cm long and only bipinnately compound. The smallest leaves are simple structures with entire margins. Leaves of the latter type occur around the buds and are similar to the cataphylls of living plants.

The roots of *Callistophyton* are protostelic and diarch (Fig. 2, 6), with exarch maturation of the primary xylem. Some roots are much branched (Fig. 35, 105), but others extend for some distance with no evidence of branching. Rooting structures range from minute rootlets to mature specimens up to 1.2 cm in diameter. When attached, the roots always occur at the nodes of the stem and are subtended by a branch or bud (Fig. 35, 105). No primary rooting system has been observed.

Branching in *Callistophyton* is axillary, with either a branch or bud present at every node (Fig. 10, 17, 34). Since the roots are borne in the axils of buds and branches (Fig. 105), serial sections passing distally through a nodal region (Fig. 106-109) encounter the departing leaf trace (Fig. 106) followed by the axillary bud or branch (Fig. 107). This is then followed by the departing root traces (Fig. 108, 109). Several specimens are preserved with no leaves attached, and only axillary branches or buds remain to mark the position of the nodes (*i.e.* CB-S-31). Buds of this type have been interpreted as adventitious (Delevoryas and Morgan, 1954), but the former position of the leaf is indicated by a subtending leaf trace that departs from the stele, traverses the secondary vascular tissue, and terminates in the periderm. Some specimens (*i.e.* CB-S-11) bear buds in the leaf axils and therefore appear to be unbranched. Others bear branches at nearly every node and probably represent much branched plants (*i.e.* CB-S-9); especially when the internodal distances are short. Many larger stems with abundant secondary tissues bear branches and buds that are oriented at approximately right angles to the parent axis. Specimens of this type often exhibit profusely branching root masses at the nodes, but leaves are usually absent (*i.e.* CB-S-31). Other stems bear branches and buds that diverge from the stem at a much smaller angle. Some of these specimens have relatively short internodes and usually show no evidence of roots at the nodes (*i.e.* CB-S-9). Many of the smallest stems with only a small amount of secondary tissue have long internodal distances with a small leaf present at each node. In these specimens buds rather than branches are usually present at each node and roots are frequently also present (*i.e.* CB-S-11). Other small stems have rather short internodes and axillary branches extend from some of the nodes.

Plant Habit

The overall structure and habit of *Callistophyton* is illustrated in Text Fig. 1. In this reconstruction *Callistophyton* is depicted as a small, understory plant with a scrambling and shrubby habit. A relatively small size is implied by the small diameter of all known stem and leaf specimens. The largest stem specimen (*i.e.* CB-S-13) is only 3.0 cm in diameter while the largest leaf probably did not exceed 25 - 30 cm in length. The long internodes and highly dissected leaves are like those of many extant plants that grow in shaded, understory habitats. The large horizontally disposed axis in the foreground produces buds and branches at right angles. The much-branched portion of the plant in the background represents those specimens with numerous axillary branches and relatively short internodal distances. The one branch of this specimen that extends into the foreground has small leaves and is unbranched. Other features that suggest a somewhat scrambling habit are adventitious roots borne at many nodes, and the small spines present at the outer margin of the primary cortex of the Middle Pennsylvanian specimens. Leaf size and structure are based on known specimens, but the exact pinnule shape and degree of pinnule dissection are somewhat speculative. As in extant plants, leaves are not present on the older parts of the stems and branches.

Stem

The stem is composed of a parenchymatous pith surrounded by axial bundles and leaf traces (Fig. 44, 47). The primary cortex consists of an inner zone of thin-walled parenchyma and an outer zone of longitudinally oriented fibrous bundles with interposed parenchyma (Fig. 11, 17, 18). In older stems, secondary xylem, vascular cambium and secondary phloem surround the pith and primary xylem (Fig. 1, 5, 33-35). Periderm is initiated within the inner primary cortex (Fig. 40), and in the most mature specimens this tissue forms the outermost zone (Fig. 23, 33, 42, 43).

Pith - Pith occupies the center of *Callistophyton* stems, and is characteristically angular in transverse section (Fig. 44). In typical internodal sections the pith is roughly triangular (Fig. 11), with leaf trace bundles occupying the corners of the triangle. In sections closer to the node the pith becomes elongated opposite the departing leaf trace (Fig. 23), and at the node the elongation is often quite pronounced (Fig. 10, 17). The pith is composed of thin-walled parenchyma with occasional interspersed cavities (Fig. 44, 47). Pith cells are polygonal and isodiametric in transverse sections, and measure 30-100 μ in diameter. In longitudinal sections the cells are axially elongated and aligned, and exhibit transverse or obliquely oriented end walls. Some pith cells in the Middle Pennsylvanian specimens contain amber contents (Fig. 18). This feature may indicate a storage or secretory function, or the dark cellular contents may merely reflect preservational factors. Pith cells in specimens of *C. poroxyloides* are typically devoid of contents (Fig. 44). Oval or spherical sacs surrounded by an epithelial lining are present in the pith (Fig. 26). These structures are referred to as secretory cavities by previous workers (Delevoryas and Morgan, 1954; Stidd and Hall, 1970b). Individual sacs measure about 200 μ in diameter. Cells of the epithelial lining are elongated parallel to the margin of the cavities, and measure up to 100 μ in greatest dimension. Amber colored deposits are often present within the sacs (Delevoryas and Morgan, 1954; Delevoryas, 1956).

Primary xylem - The primary xylem is represented by axial bundles and leaf traces located at the margin of the pith (Fig. 44, 47, 106). In Middle Pennsylvanian specimens the bundles usually appear as separate and discrete units in transverse sections (Fig. 47). The number of bundles present in transverse sections ranges from 9 at the base of an internode, to 11 near the level of the next node above (Text Fig. 2). At the level of leaf trace departure from the stele, 13 bundles are present in transverse section Individual bundles vary considerably in considerably in size, and in the number of primary xylem cells of which they are composed (Fig. 44, 47). The largest are either axial bundles in the process of dichotomizing, or leaf trace bundles. The smaller bundles are often difficult to recognize in poorly preserved specimens. Bundles of *Callistophyton poroxyloides* are typically mesarch (Fig. 26, 27), while those in the Middle Pennsylvanian specimens are exarch (Fig. 37,38). This latter feature consistently distinguishes specimens from the Upper and Middle Pennsylvanian localities. As one might expect, however, some specimens from each locality show variation with respect to the development of the primary xylem. In a few specimens of *C. poroxyloides* one observes a bundle with little or no development of the centripetal or centrifugal metaxylem. Consequently, the bundle appears to be either exarch or endarch. Likewise, in some Middle Pennsylvanian specimens a few centrifugal metaxylem tracheids are occasionally present in a bundle, which then appears to be mesarch. This phenomenon is usually only evident for a short distance along a given bundle, and does not appear to be correlated with the nodal or internodal level of section, or with the division of a bundle. It is not a characteristic of the leaf trace bundles, and is probably nothing more than a reflection of random developmental variation within the primary xylem of each type. A slender strand of parenchyma accompanies each primary bundle (Fig. 26, 39). In transverse sections the parenchyma appears as a patch with protoxylem at the inner side (Fig. 27, 38). In *C. poroxyloides* the metaxylem elements form the outer margin of the bundle, and separate the parenchymatous strand from the secondary xylem (Fig. 27). In the Middle Pennsylvanian specimens, however, the parenchyma strand is directly adjacent to the earliest formed secondary xylem elements. Metaxylem is present on only the lateral and centripetal sides of the primary bundle (Fig. 38).

Protoxylem tracheids are polygonal and isodiametric in transverse sections. They measure 12 - 25 μ in diameter. In longitudinal sections protoxylem elements have wall thickening patterns of the spiral and scalariform type (Fig. 52, 59). Metaxylem tracheids are typically larger in transverse sections, measuring 25 - 80 μ in diameter.

In longitudinal sections secondary wall thickening patterns are present on all faces, and are of the reticulate and bordered pitted types (Fig. 59). In the latter type the pits are alternate and oval with crossed, slit-like apertures (Fig. 64). Primary xylem parenchyma cells are axially elongated (Fig. 52), and isodiametric in transverse view. Individual cells are typically 4 - 8 times as long as broad and exhibit slightly oblique end walls.

Secondary Xylem - *Callistophyton* stems produce abundant secondary xylem that consists of alternating radial files of tracheids and xylem rays (Fig. 51, 58). The files of tracheids range up to 70 cells in radial extent (Fig. 10). The files are 1 - 5 cells wide with 1 - 3 cell widths occurring most frequently (Fig. 23, 33). Individual files become wider as they extend toward the periphery of the stem. After a width of 3 - 5 cells is obtained a ray is initiated to divide the file into two. Those tracheids that occur at the base of the internode and above where the traces depart are typically shorter and contorted. They are also separated by wide rays (Fig. 61). This region is similar to the reaction wood that occurs at a similar position in living conifers. Tracheids are angular in transverse sections with 3 - 6 sides (Fig. 51, 58). They are approximately 1 cm long and have tapering end walls (Fig. 56). Several rows of alternate, oval, bordered pits are present on the radial cell walls (Fig. 50, 57). The number of rows ranges from 2 - 7 in *Callistophyton poroxyloides*, and from 2 - 6 in the Middle Pennsylvanian specimens. Three to five rows is most commonly observed in both species. Well-preserved pits exhibit crossed slit-like apertures similar to those of the metaxylem (Fig. 64). The apertures appear to be oval in less well-preserved tracheids (Fig. 54). When the preservation is quite poor the radial tracheid walls exhibit a meshwork of hexagonal openings that represent the positions of individual pits (Fig. 50). No pitting has been observed on the tangential tracheid walls.

The xylem rays range from 1 - 4 cells wide, but biseriate rays are most common. The rays are extremely high (Fig. 50, 60), often exceeding the length of the tracheids in longitudinal extent. Individual rays are homogeneous and composed of thin-walled parenchyma cells (Fig. 53, 57). In tangential sections the ray cells are isodiametric (Fig. 56, 60). In radial view they are angular and range from square to rectangular, with slight radial elongation (Fig. 53, 57). The ray parenchmya cells of *Callistophyton poroxyloides* have no internal contents, but some cells in the Middle Pennsylvanian specimens contain amber material (Fig. 57). Ray parenchyma cell walls that are adjacent to tracheids often exhibit large, oblique simple pits (Fig. 62). Secondary xylem is absent from stem and bud apices.

Vascular Cambium - A narrow zone of thin-walled cells is present at the outer margin of the wood. This zone is 2 - 4 cells thick and represents the fusiform and ray initials and their most recent derivatives (Fig. 55, 63). In transverse sections the fusiform initials are tangentially elongated, while the ray initials are either isodiametric or slightly radially elongated. Comparison of several specimens with varying amounts of secondary vascular tissues reveals several aspects of vascular cambial activity. At first, the newly formed vascular cambial cells apparently cut off derivatives toward the interior only, with secondary phloem production beginning somewhat later. In specimens with approximately 5 - 10 rows of secondary tracheids, the first formed secondary phloem cells are present. In the largest specimens with well-preserved secondary phloem, the number of radial files of phloem cells is only slightly smaller than the number of xylem cells. This suggests that after the initiation of secondary phloem production the cambial cells produce xylem and phloem cells in nearly equal numbers. This latter feature is not always apparent, however, since the larger size of the tracheids creates a thicker secondary xylem zone (Fig. 23, 33).

Phloem - In *Callistophyton*, as in many other fossil plants, the position of the primary phloem is difficult to establish with certainty. There are, however, some indications of primary phloem in several well-preserved specimens. In transverse sections of some immature stems there are large cells accompanied by very small cells (Fig. 102, at arrow). These occur just exterior to the primary xylem bundles. In more mature specimens the radial files of phloem cells extend inward from the smallest cells in these areas (Fig. 63). These small cells may, therefore, represent primary sieve cells.

The secondary phloem consists of radial files of sieve cells and phloem parenchyma that are interspersed with phloem rays (Fig. 55, 63). In transverse sections the sieve cells are large and slightly tangentially extended. In longitudinal view the sieve cells are extremely elongated with tapering end walls. Well-preserved sieve cells exhibit regularly spaced amber masses along their longitudinal walls. These masses have been interpreted as probable callose plugs in the sieve areas (Delevoryas and Morgan, 1954a). The phloem parenchyma cells are much smaller, and in transverse view are seen as tangentially oriented chains of 2 - 5 cells that alternate with the sieve cells (Fig. 55, 63). In longitudinal sections the phloem parenchyma cells are axially elongated similar to the primary xylem parenchyma cells. Examination of the most recently formed secondary phloem cells reveals that the tangentially oriented rows of phloem parenchyma originate by subdivision of the fusiform derivatives that alternate with potential sieve cells (Fig. 55, near cambium). The phloem rays occur opposite xylem rays, and extend radially; becoming progressively wider toward the outer margin of the zone (Fig. 63). Some of this increase in width is due to tangential extension of the ray parenchyma cells. This probably occurs in response to an increasing diameter in the growing stems. Phloem ray cells are similar to the xylem ray cells, but are somewhat larger (Fig. 42). At the outer margin of the zone phloem ray parenchyma cells intergrade with the cells of the inner cortex (Fig. 63). In some of the larger Middle Pennsylvanian specimens the phloem cells toward the exterior of the zone exhibit thickened walls and dark internal contents (Fig. 43). These cells are similar to the sclereids that form in the phloem of many living plants. Enlarged cells are present in the secondary phloem of well-preserved specimens when viewed in transverse sections (Fig. 55, 63). Many of these replace a tangential row of phloem parenchyma cells, but others are found in the positions of sieve cells. Cells of this type are filled with dark contents and appear to be resin canals when viewed in longitudinal sections (Fig. 53). On close examination, however, cross walls of the cells can usually be identified. Other enlarged cells with dark contents are spherical or ovoid in both longitudinal and transverse sections. Cells of this type appear similar to the secretory cavities of the pith, but are not surrounded by an epithelial cell layer.

Cortex - Young specimens of *Callistophyton* have a primary cortex composed of a thick parenchymatous inner zone, and a thinner sclerenchymatous outer zone (Fig. 19, 28). Cells of the inner cortex are thin-walled and isodiametric. In transverse sections of Middle Pennsylvanian specimens the cells of the inner cortex measure 30 - 90 μ at the inner margin of the zone, and grade to a somewhat smaller size toward the outer margin (Fig. 18). In specimens of *C. poroxyloides* no gradation of cell size is present, but noticeably larger cells are present. These occur with a greater frequency toward the outer margin of the zone (Fig. 96). In longitudinal sections the cells of the inner cortex are isodiametric and either randomly arranged, or somewhat vertically aligned. Dark contents are present within some cells of the Middle Pennsylvanian specimens, but are absent from the cortical cells of *C. poroxyloides* (Fig. 40, 102). The outer sclerenchymatous cortical zone is composed of longitudinally oriented fiberous bundles and interposed parenchyma. The thick-walled cells are elongated parallel to the axis, while the thin-walled cells are like those of the inner cortex. The extent of fiberous bundle formation is quite variable among the specimens from each locality. In some specimens the fibrous bundles are poorly developed and inconspicuous (Fig. 28), while in others they appear as well formed and discrete bundles (Fig. 96). In still other stems they are laterally fused forming a nearly continuous cylinder of thick-walled cells (Fig. 34). Within a single specimen the extent of fibrous bundle formation may vary at different levels. In longitudinal sections the fibrous bundles are disposed in a relatively parallel manner with infrequent anastomoses. Specimens with a small amount of secondary xylem exhibit a discontinuity between the inner and outer cortical zones (Fig. 41). In specimens with a larger amount of secondary wood the inner cortex is either crushed or absent (Fig. 21, 29). This suggests that the initial increase in stele diameter due to secondary development is accommodated by a reduction in the thickness of the inner primary cortex, and accounts for the presence of unbroken outer primary cortex on stems with several rows of secondary tracheids (Fig. 20, 34). In the largest specimens the fibrous primary cortex is disrupted or entirely absent (Fig. 23, 33).

Enlarged cavities like those of the pith occur within the cortex of most specimens (Fig. 34). Some of the enlarged cells in the inner cortex of immature *Callistophyton poroxyloides* stems may represent incompletely formed cavities of this type (Fig. 102). In the outer cortex of the Middle Pennsylvanian specimens some of the cavities are greatly enlarged with up to three cell layers of epithelial lining (Fig. 34).

In well-preserved specimens a uniseriate epidermis of isodiametric, thin-walled cells is present at the outer margin of the cortex (Fig. 102). Cortical appendages are present at the outer margin of some well-preserved stems. However, the frequency of these appendages is quite variable. Some specimens exhibit numerous appendages in cross sections, while others appear to have only a few. Still other stems appear to be devoid of these structures. This may be due in part to destruction of the appendages on some specimens prior to fossilization. The appendages of *C. poroxyloides* have been described as stalked glands (Delevoryas and Morgan, 1954). This is due to a rather restricted basal zone, and an enlarged apical region composed of large, thin-walled cells (Fig. 24, 25). These glands are quite similar to those present on specimens of *Lyginopteris* and its associated organ genera (Oliver and Scott, 1904). Individual appendages measure up to 200 μ long. Cortical appendages present on many of the Middle Pennsylvanian specimens are larger than those of *C. poroxyloides*. They are also distinctively shaped with an enlarged basal zone of large cells, and an acutely pointed apex composed of smaller, thicker-walled cells (Fig. 36). Appendages of this type measure up to 700 μ long, and are more like small spines than capitate glands.

Periderm - A thin zone of periderm is present at the outer margin of the inner cortex in specimens with a small amount of secondary xylem. This zone is typically separated from the outer margin of the secondary phloem by 5 - 10 cell layers and becomes detached from the outer zone of the primary cortex (Fig. 41). Periderm initiation probably occurs in the midregion of the inner primary cortex (Fig. 40), with the concurrent or subsequent destruction of more peripheral inner cortical cells by the lateral expansion of the stele. The periderm in specimens of this type typically consists of 3 - 6 cell layers of radially aligned, thin-walled cells (Fig. 41, 42). Periderm initiation may occur earlier at one side of the stem than at the other (Fig. 18) (Delevoryas and Morgan, 1954), but in specimens with abundant secondary xylem periderm is present at all points around the margin of the stem (Fig. 23, 33). In many stems with abundant secondary growth the periderm is only a few cell layers thick (Fig. 1, 5). Some of the largest specimens, however, exhibit a thick zone of periderm (Fig. 23). In transverse sections of these latter stems the periderm is of uneven thickness with a very rough outer margin (Fig. 33). The individual peridermal cells are also randomly disposed, which suggests a periderm development similar to that of *Medullosa* (Delevoryas, 1955). In the latter genus a definite phellogen is present at early stages, but later divisions occur within the individual cells. Periderm cells are isodiametric in both transverse and longitudinal sections, and exhibit little or no vertical alignment (Fig. 53, 65, at right). The cells of this zone are usually devoid of contents, but in the largest Middle Pennsylvanian specimens dark cell contents are present (Fig. 65). Black areas are seen in the periderm when viewed in transverse sections. In longitudinal view these areas appear similar to the resin canals of other Carboniferous pteridosperms, but on closer examination are seen to consist of somewhat enlarged angular cells that are vertically aligned and filled with dark contents (Fig. 53, at right).

Foliage

Callistophyton foliage frequently occurs in association with stem specimens. Entire fronds are occasionally connected to the stems, but more often only petiole bases are found attached. The attached fronds are always small, measuring about 4 - 8 cm long. Many of the attached petiole bases, however, are up to 4 - 5 times as large as the bases of the entire leaves (Comp. Fig. 73, 74). These larger leaves were, therefore, probably as much as 25 - 30 cm long. Individual fronds are typically bi-, tri-, or quadripinnately compound with laminar pinnules. Dichotomously branched rachises are not typical of *Callistophyton* fronds (Delevoryas, 1956; Stidd and Hall, 1970b), but the occurrence of one Middle Pennsylvanian specimen with a dichotomizing rachis (Fig. 76) establishes the presence of this feature in the genus. The remainder of the frond dissection is pinnate, with the successive orders of pinnae born in two ranks, and at nearly right angles to the parent order of branching (Text Fig. 1). Immature fronds are found attached to bud and branch apices (Fig. 90-101), and can also be identified when isolated (Fig. 84). Fronds of this type exhibit circinate vernation, with all orders of pinnae coiled toward the adaxial surface.

The glandular cavities that are characteristic of the ground tissue of *Callistophyton* organs are typically quite prominent in these crosiers (Fig. 84, 94, 100).

In transverse sections of mature specimens the rachis typically consists of a somewhat adaxially arched, band-shaped trace surrounded by inner and outer cortex like that of the stem (Fig. 3, 4, 16). The trace of a few specimens is, however, abaxially arched (Fig. 73). This may be due in part to crushing of the specimen. In basal sections, and at the levels of primary pinnae trace divergence, some specimens exhibit a trace that consists of two adjacent bundles (Fig. 16, 82) (Delevoryas and Morgan, 1954). Individual traces of the Middle Pennsylvanian specimens have protoxylem elements positioned at the adaxial surface of the trace, but discrete strands are difficult to distinguish in all but the most basal sections (Fig. 83). Protoxylem elements of *Callistophyton poroxyloides* occur in the center of the trace, thus reflecting the mesarch primary xylem development in this species. Secondary xylem is present in the rachis as a continuous band of tracheids positioned at the abaxial margin of the trace (Fig. 3, 4, 74). In one specimen, however, the secondary xylem is divided into two adjacent strands. This is probably due to incomplete preservation. In some specimens the secondary wood is present at the petiole base only, but in others it is found in sections distal to where the first primary pinnae traces are produced (Fig. 83). In still other specimens no secondary tracheids are present at even the most proximal levels (Fig. 16). This latter condition may be due to the immaturity of these specimens, but is more likely merely a reflection of the ephemeral nature of some leaves. The presence of phloem is difficult to determine in most foliar specimens. In leaf traces located in the cortex of the stem, however, phloem can be located at the abaxial margin of the trace (Fig. 82). The leaf traces of *C. poroxyloides* have been questionably interpreted as concentric bundles (Delevoryas and Morgan, 1954). In the present study, however, evidence of phloem at the adaxial margin of the trace has not been found in any Middle Pennsylvanian specimens or any fronds of *C. poroxyloides*. *Callistophyton* traces are therefore considered to be collateral bundles.

Primary pinnae traces are produced at the lateral margins of the petiole trace (Fig. 83). Individual primary pinnae traces are band-shaped in transverse sections (Fig. 83). No secondary xylem has been observed accompanying the traces of the primary pinnae or higher orders of pinnae.

Mature pinnules are characteristically much bent and contorted in the coal-ball material. Exact pinnule shape is therefore difficult to establish. Nevertheless, several structural features of the pinnules can be determined by examination of peel preparations. In transverse sections, individual pinnules typically exhibit a prominent midvein with lamina attached to the lateral margins (Fig. 75, 78).

In paradermal view the pinnules are always incomplete, but sections do reveal that they are deeply lobed (Fig. 85). The lobes are either rounded or bluntly pointed (Fig. 85). At the base, each pinnule is constricted to a rather narrow point of attachment. A single midvein enters the base of each pinnule, and diminishes in prominence toward the tip. Each lobe is vascularized by a single vein that departs from the midvein at a sharp angle, and dichotomizes 2 - 4 times toward the margin (Fig. 86). The veins have elongated tracheids with spiral and scalariform wall thickening patterns. Veins are typically either imbedded within the thin-walled mesophyll (Fig. 75, 79), or supported by ad- and abaxial sclerenchyma (Fig. 81). In one specimen, however, a layer of cells with dark internal contents surrounds the veins (Fig. 80). This layer may represent a weakly differentiated bundle sheath, or may be merely the result of unusual preservation. Between the veins, the lamina of some specimens consist of relatively tightly packed and thin-walled mesophyll cells (Fig. 75, 80). In paradermal view the mesophyll cells of these specimens usually appear isodiametric and randomly oriented (Fig. 87). In some areas, however, a weakly developed, uniseriate palisade layer is present adjacent to the adaxial epidermis (Fig. 77). In other specimens thick-walled sclerenchyma cells are present above and below the midvein, and in some or all of the lateral veins (Fig. 81). In specimens of this latter type the cells near the adaxial margin are tightly packed, but those toward the abaxial surface form weakly developed plates of cells that extend at right angles to the veins and are separated by large lacunae (Fig. 88, at bottom). A uniseriate epidermis of isodiametric cells is present on well-preserved pinnules (Fig. 79, 80). On most specimens, however, this layer is poorly preserved and inconspicuous (Fig. 81). In paradermal view, epidermal cells are isodiametric and randomly oriented between the veins, and slightly elongated in areas adjacent to the veins (Fig. 89). Stomata have not been observed. The epidermis of immature specimens is clothed in a dense mass of uniseriate, multicellular hairs (Fig. 97-104). On more mature specimens the hairs are typically absent, but a few hair bases have been observed on the abaxial surface of some pinnules. Glandular cavities like those of the stem are present in the ground tissue and mesophyll of all frond segments (Fig. 84-88).

Among presently known compression form genera of Pennsylvanian fern-like foliage, the above pinnule features suggest similarities to *Sphenopteris* (Brongniart) Sternberg (1825), or *Mariopteris* Zeiller (1879). Common features of *Callistophyton* foliage and some species of each of these include a lobed outer margin, a constricted base, and a single, prominent midrib that enters the pinnule base and diminishes toward the distal margin. In general frond structure, *Callistophyton* foliage is typically pinnately divided like *Sphenopteris* type fronds. *Mariopteris* leaves exhibit dichotomous branching of the rachis and primary pinnae, and sometimes the higher order of pinnae as well. If found in the compressed state, *Callistophyton* foliage would therefore most likely represent a species of *Sphenopteris*.

Buds and Branches

Appendages present at the nodes of *Callistophyton* grade from small buds, to large branches that exceed the diameter of the stems on which they are borne (Fig. 34). In one specimen the stem apex is represented by a small apparently dormant bud, while the axillary branch has grown into a large structure with abundant secondary tissue. A bud or branch is present at all the nodes in all known specimens. The smallest buds consist of a parenchymatous mound of tissue with two oppositely-placed, scale-like leaves or cataphylls (Fig. 103-104). Internally, there is no evidence of tissue differentiation. The leaves are borne at right angles to the plane of bud divergence from the stem, and therefore appear to be positioned at the sides of the bud (Fig. 103). Distally the leaves extend beyond the bud apex (Fig. 104). Both the bud apex and the scale leaves are clothed in a mass of multicellular hairs identical to those described on immature leaves. Somewhat larger buds bear a larger number of leaves in a spiral arrangement. Examination of leaf position and the divergence angles of successive leaf traces suggests that the first two leaves are in a 1/2 arrangement (Fig. 90). Subsequent leaves are apparently arranged in a 1/3, and then a 2/5 phyllotactic spiral. The bud axes exhibit very short internodes at the base; the first six leaves often occurring within a distance of 5 mm or less.

The apical region of the buds and branches is constructed of a homogeneous mass of thin-walled cells (Fig. 105), which presumably represent a region of promeristem. Although the absence of well-preserved, mid-longitudinal sections of this area leaves the exact histology of the meristem somewhat questionable, available sections suggest that the first 1 - 3 cell layers at the apex are oriented parallel to the surface. The adjacent cells appear to be isodiametric and randomly disposed as in the promeristems of many living seed plants (Esau, 1960).

In somewhat more proximal transverse sections procambium can be identified (Fig. 91, 99). This grades proximally into a region where pith, primary xylem and cortex are evident (Fig. 90, 96, 102). At still more proximal levels secondary tissues are present (Fig. 40). The largest specimens are regarded as axillary branches and are like the previously described stems at all but the most proximal levels. The basal scale-like leaves are typically absent from the axillary branches, but closely spaced leaf traces can be identified in section view. Specimens with five or more leaves usually exhibit secondary xylem and phloem at the proximal levels. This indicates that no subsequent internodal elongation takes place in this region. Primary xylem is difficult to identify in the base of all but the most well-preserved specimens (Fig. 107). More distally, the secondary tissues decrease in thickness, and the primary xylem strands become larger and more readily identifiable. The first 4 - 6 leaves produced at the base of the buds and branches are small and entire, but subsequently produced fronds exhibit pinnate dissection like the previously described foliar material (Fig. 104, 90-95).

The *Callistophyton poroxyloides* stem apex described by Delevoryas (1956) was also studied in this investigation. The specimen can be distinguished from an isolated axillary bud by several features. All the preserved leaves of the bud are pinnately compound structures, and are in an apparently 2/5 arrangement (Fig. 100, 101). There is also some distance of internode preserved below the bottom of the most proximally attached leaf (Fig. 96). The primary body is immature throughout the specimen, and at only the most proximal levels are even protoxylem elements developed (Fig. 96, 102). These features suggest that a significant amount of internodal elongation is possible at the base of the apical bud. The long internodal distances present in several more mature stems indicate that a large amount of internodal elongation did in fact take place in many specimens. When viewed in transverse sections the procambium of *Callistophyton poroxyloides* appears as a cylinder, rather than a ring of isolated bundles (Fig. 96).

This is probably due to the fact that the mature primary bundles of this species are laterally adjacent. In comparable sections of the Middle Pennsylvanian *Callistophyton*, where the bundles are not laterally confluent, one would expect to see a ring of procambial strands.

Roots

The roots of *Callistophyton* have not previously been reported. The specimens described here are in this account are often attached in the axils of buds or branches (Fig. 105), but can also be identified when isolated. Roots may be as large as the stem that bears them (Fig. 35), but are usually much smaller (Fig. 108, 109). The largest known root specimen (Fig. 2) is assignable to *C. poroxyloides* stems, and measures 1.2 cm in diameter. This, and other large roots (Fig. 6) exhibit abundant secondary tissue. The remainder of root specimens grade in size to minute rootlets with no evidence of secondary development (Fig. 109). Some specimens branch profusely (Fig. 105) especially near the base. Others are apparently sparsely branched beyond the most basal levels. Branching is initiated opposite one of the two protoxylem points (Fig. 110), but no other consistent frequency or sequence of branching is evident.

In transverse sections individual roots are exarch and diarch (Fig. 2). The primary xylem is surrounded by a zone of thin-walled cells that represent primary cortex

(Fig. 111). No primary phloem or endodermis could be identified. This may be due in part to the imperfect preservation of the small *Callistophyton* roots (Fig. 111). Cells of the cortical region are isodiametric in transverse sections, and some contain dark contents (Fig. 105, 111). In longitudinal sections these cells are rectangular, and axially elongated 3 - 4 times their diameters. Cells with dark contents are often vertically aligned and superficially appear as resin canals. The outermost 1 -- 2 cell layers can be distinguished by an absence of internal contents, and may represent a poorly differentiated epidermis (Fig. 111, at arrow).

Larger roots typically exhibit abundant secondary tissues (Fig. 35, 105). Secondary xylem is like that of the stem, except opposite the protoxylem strands (Fig. 2, 6, 111). In these areas conspicuously large rays are produced in the place of radially aligned segments of tracheids (Fig. 2). In transverse sections these rays dissect the secondary wood into two distinct regions (Fig. 6). Vascular cambium and secondary phloem like that of the stem surrounds the secondary xylem. This is in turn surrounded by a few layers of cortical cells, and periderm (Fig. 2, 6). In the Middle Pennsylvanian specimens many of the cortical cells are conspicuously large (Fig. 2) and distinct in transverse sections. This feature has not been observed in the roots of *C. poroxyloides*. The periderm is composed of several layers of radially aligned, thin-walled cells (Fig. 2). In some specimens the periderm forms a continuous cylinder at the exterior of the root. In others, however, the periderm appears to be broken into segments when viewed in transverse sections. The segments are most widely separated at their outermost points, and are, therefore, probably broken apart by an increasing stem diameter. The periderm apparently originates in the mid-region of the primary cortex. This is evidenced by specimens with a small amount of secondary xylem. In these, the primary cortex is delimited into inner and outer zones, which are separated by a cellular discontinuity. The outermost 1 - 2 cell layers of the inner cortex of these specimens probably represent the first formed periderm cells. Periderm development is probably from a definite internal phellogen as evidenced by the radial alignment of peridermal cells. In this respect the development of the root periderm differs from the periderm in older stems.

Primary Vasculature

The primary vasculature of *Callistophyton poroxyloides* is described as consisting of leaf traces that enter the stem and pass basipetally (Delevoryas and Morgan, 1954). The number of bundles seen in stem cross sections is described as about 9. Individual traces are double stranded near the base of the leaf, and single stranded at more proximal levels.

The primary vascular system of *C. poroxyloides* and the

Middle Pennsylvanian specimens have been examined in this study, and are found to be essentially the same (comp. Fig. 44 and 47). The vascular system is interpreted as consisting of independent axial bundles or sympodia, and leaf traces. The sympodia extend axially through the stem, and each produces leaf traces. This is similar to the structure of many seed plants including *Lyginopteris*, *Archaeopteris* and those extant conifers with spiral phyllotaxy (Scott, 1923; Namboodiri and Beck, 1968a; Beck, 1970). The terminology and leaf numbering system used is consistent with that of Namboodiri and Beck (1968a). In the preparation of vascular system reconstructions the most distal leaf is assigned the lowest number, and more proximal leaves are assigned progressively higher numbers. Consequently, the earliest formed leaves, which one would expect to have the lowest numbers, are those with the highest numbers. This seeming inconsistency is the result of a convenient numbering system for the study of stem apices, and can be somewhat confusing when trying to interpret mature stem specimens. It is, however, used in the present study so that one can readily make comparisons with previously described material. *Callistophyton* stems are examined in transverse section, with serial sections (Text Fig. 2) used to construct a composite diagram of the vascular system. Unfortunately, because of imperfect preservation of some stems and the long distance between nodes of others reconstruction of the primary vascular system cannot be made from any single

Text Fig. 2. Primary vascular structure of *Callistophyton*. Short segment of stem illustrating the pattern of bundle division between two nodes. Longitudinal diagram of bundles at center; numbers above bundles indicate successive leaf traces. Lines above leaf traces indicate vascular tissue to axillary buds or branches, and to adventitious roots. Serial transverse sections of stem, at left, to illustrate the primary bundle pattern at the indicated levels (CB-S-11). Transverse sections of stem, at right, to illustrate the primary bundle pattern in the Autun material (redrawn from Bertrand and Renault, 1886b). See text for more complete explanation.

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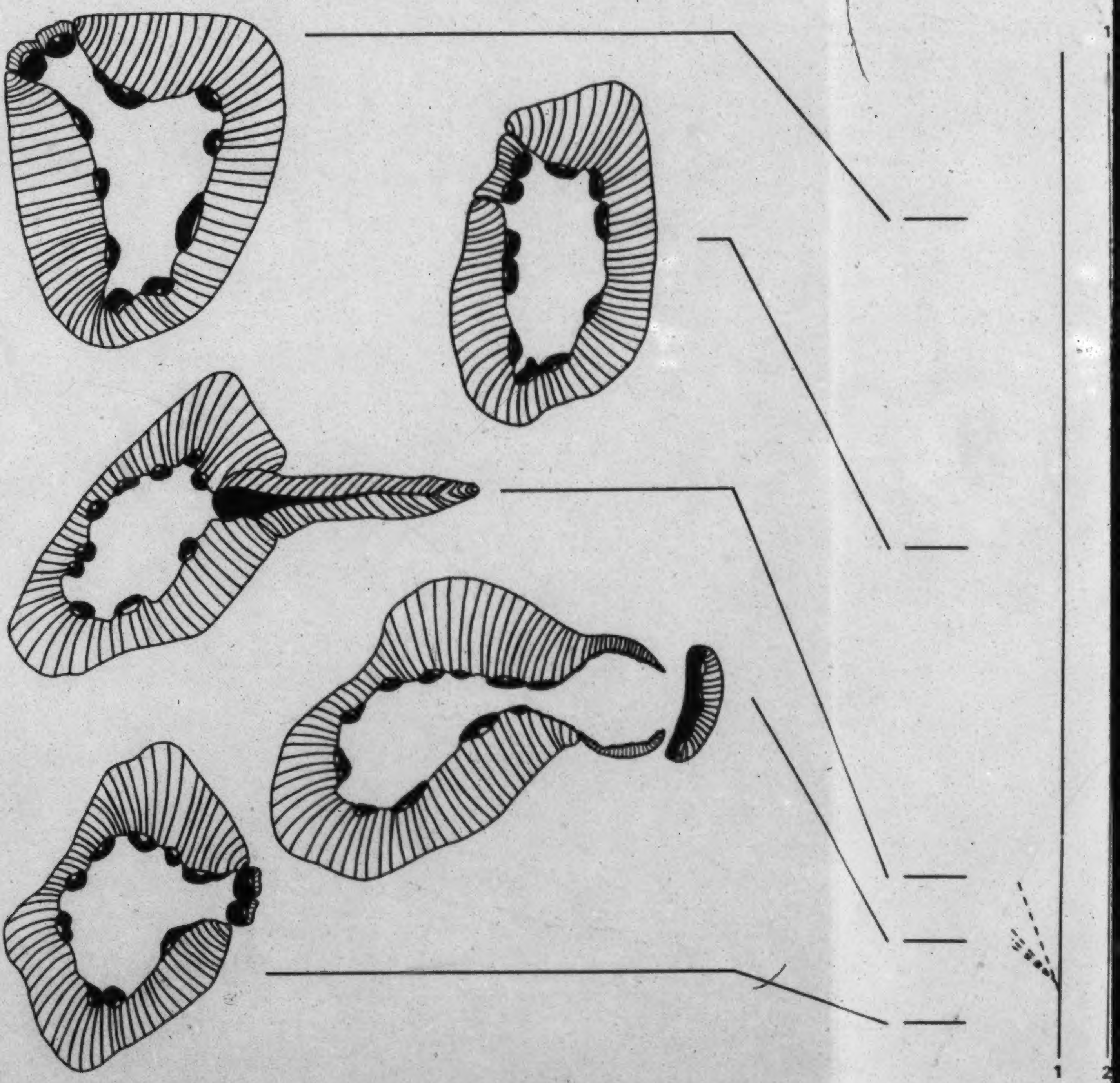
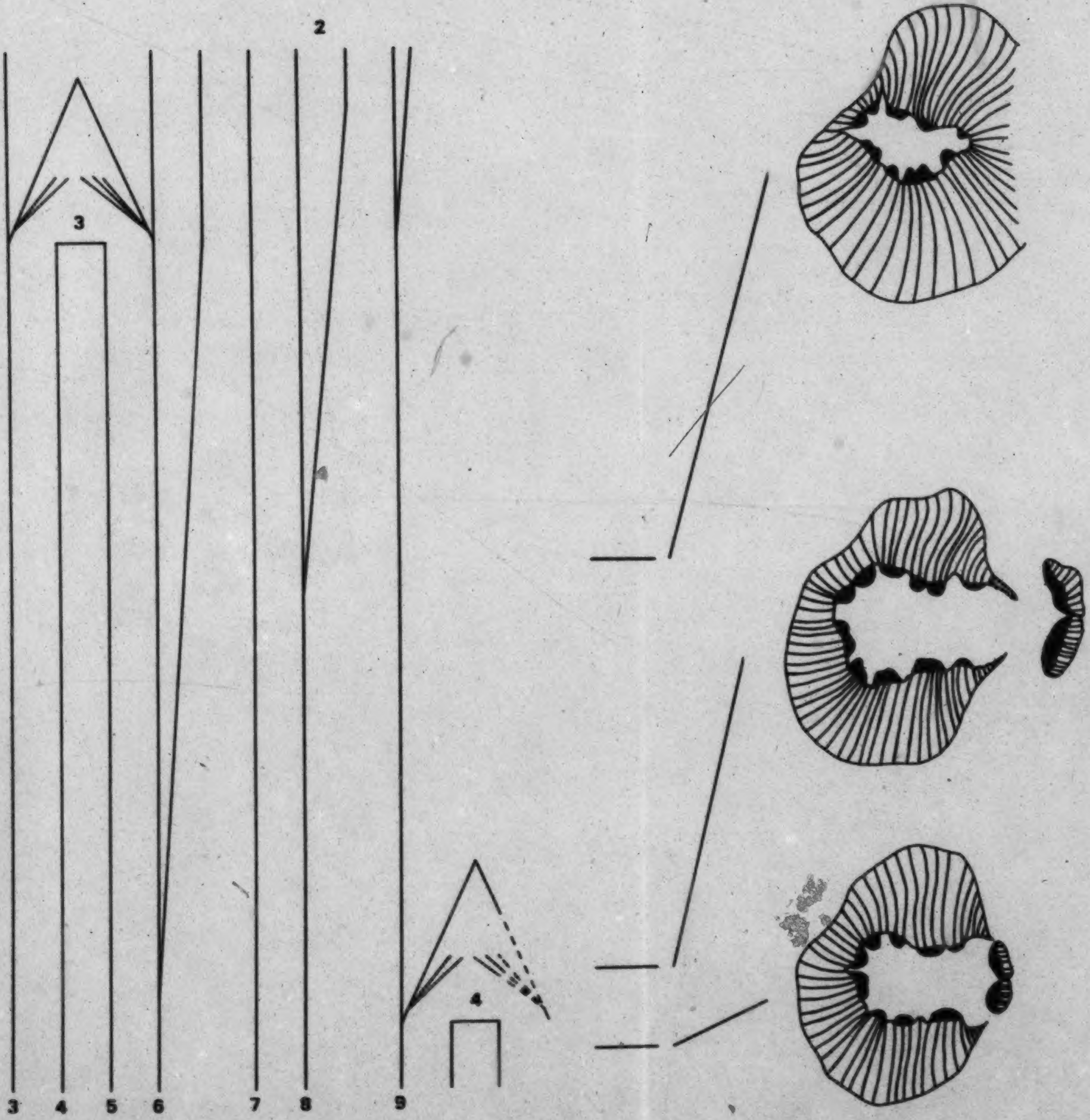
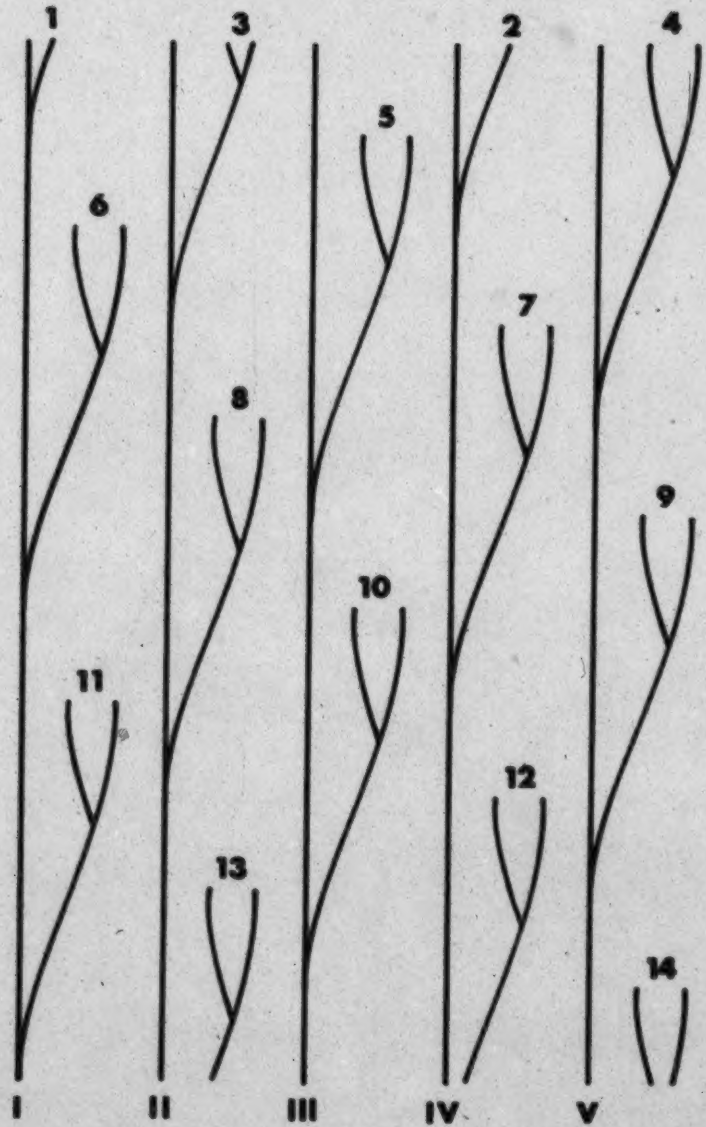




specimen. To prepare such a diagram the pattern of the vascular bundles in short segments must first be determined. If a consistent pattern is found, it may be superimposed upon itself to reveal the structure of the vascular system. In Text Fig. 2 (at left) a specimen with two departing leaf traces is depicted as if the vascular cylinder were split open next to the departing leaf trace at the lower node, and layed out flat with the outer surface facing the observer. In this view nine bundles and a double leaf trace are present at the lower node. If the bundles are numbered 1 - 9 from left to right, the following pattern is observed. Bundles 1 - 3, 7 and 9 extend undivided to the node above. Bundle 6 divides near the base of the internode, and bundle 8 divides somewhere in the mid-region of the internode. Bundles 4 and 5 form the double trace of the leaf that is given off at the upper node. This pattern is consistent for all Middle and Upper Pennsylvanian specimens examined. Thus, if one assumes that the pattern between any two nodes is consistent within a single specimen, as it is in several other previously described seed plants (*e.g. Lyginopteris*, Scott, 1923; *Stenomyelon*, *Calamopitys*, Callixylon, Beck, 1970; several extant conifers, Namboodiri and Beck, 1968a, 1968b), then the primary vascular structure can be reconstructed. Text Fig. 3 represents the reconstruction of a section of vascular system composed of several nodes and internodes, and shows evidence of 14 leaf traces. The vasculature is seen to consist of 5 axial bundles (Roman

Text Fig. 3. Axial vascular system of *Callistophyton*. The diagram is constructed by splitting the stem open next to a sympodium and laying it out flat with the outer surface facing the viewer. The system consists of five sympodia (Roman numerals at bottom), and leaf traces that are numbered consecutively from top to bottom.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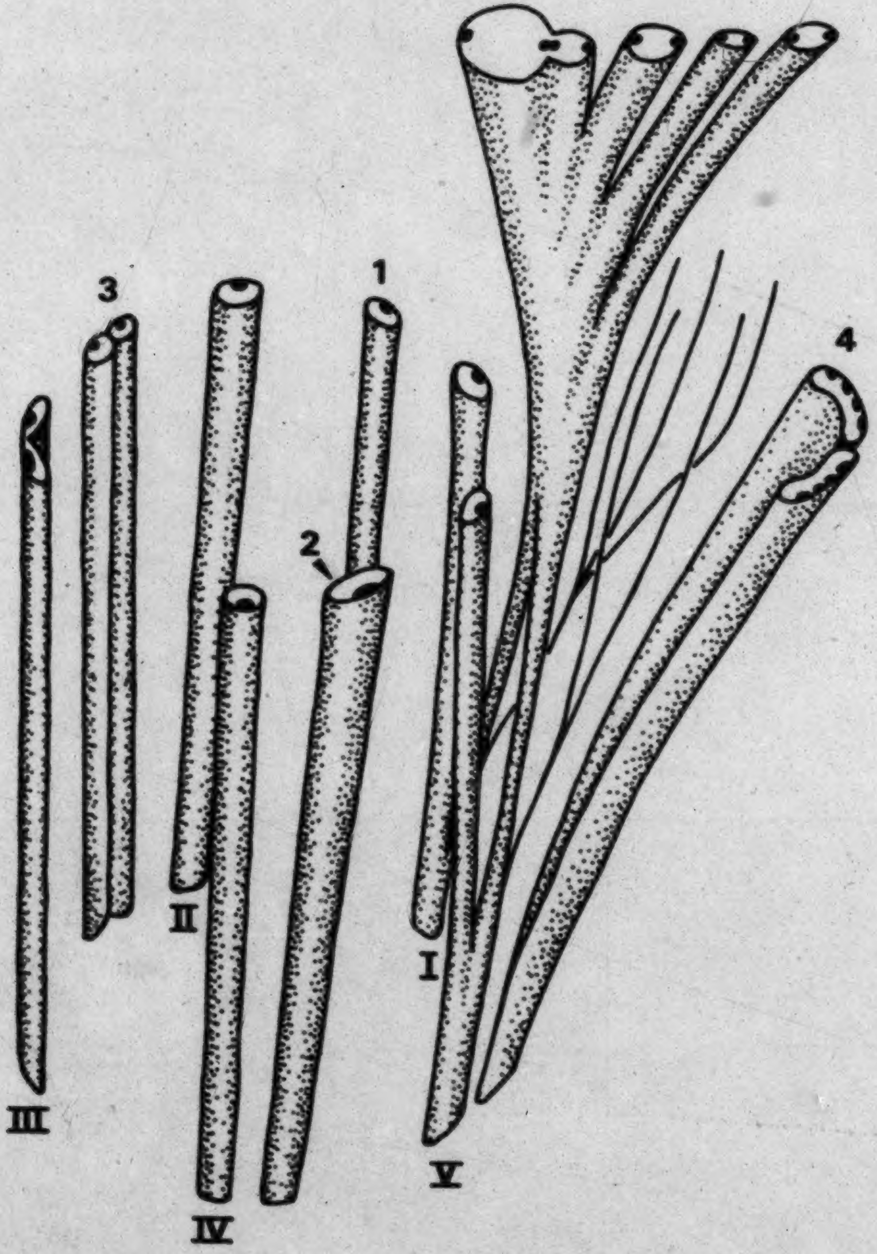
numerals in Text Fig. 3) that produce leaf traces in a 2/5 phyllotactic spiral (*i.e.* leaf trace #1 is directly above leaf trace #6; trace #2 is above trace #7; *etc.*). In transverse sections of stem specimens the division of an axial bundle to produce a leaf trace is first recognized by an enlargement of the bundle and by the division of the protoxylem strand (Text Fig. 2). This is followed by a dichotomy of the bundle to form the leaf trace. The axial bundle continues distally for 5 nodes before again dividing to produce another leaf trace (Text Fig. 3). The leaf trace extends through approximately two and one half internodes and then divides to produce a double trace (Text Fig. 3). This double trace continues through another one and one-half internodes before entering the base of the leaf. Each leaf trace is, therefore, recognizable at a level that is four nodes below the base of the leaf it supplies (Text Fig. 3). The direction of leaf trace divergence and the direction of ontogenetic spiral are the same (Text Fig. 3). This is consistent with the pattern in *Lyginopteris* (Scott, 1923; Beck, 1970), and those extant conifers that have 5 sympodia (Namboodiri and Beck, 1968c). The direction of spiral in *Callistophyton* is typically dextrorse (to the right in Text Fig. 3), but a few specimens exhibit a sinistrorse (to the left) spiral. One stem with a dextrorse spiral produces a bud with a sinistrorse spiral indicating that the difference is not of taxonomic value.

A reconstruction of *Callistophyton* nodal vasculature is presented in Text Fig. 4. At the level of leaf trace divergence those bundles that flank the departing leaf trace (Fig. 48, at large arrow points) undergo an unequal division (Text Fig. 2, 4). The smaller segment is produced toward the departing leaf trace. These two bundles extend distally in the axil of the leaf trace, and fuse to form the vascular tissue in the base of the root mass (Fig. 108, Text Fig. 4). Before the bundles fuse, however, each gives off a few tracheids that extend into the base of the axillary bud or branch (Fig. 48, at small arrow points; Text Fig. 2, 4). For the sake of clarity these are depicted as discrete bundles in the text figures. In the actual specimens discrete bundles are difficult to identify below the fourth or fifth node of the bud or branch (Fig. 49). At nodes of the stem where no roots are present the two strands diminish in size and terminate in the cortex above where the tracheids are given off to the base of the bud or branch.

Text Fig. 4. Stereo diagram of nodal vasculature with a leaf trace diverging at right. Sympodia are indicated by Roman numerals at bottom, and agree with those in Text Fig. 3. Leaf traces are indicated by numbers at the top, and also agree with those in Text Fig. 3. Note the origin of traces to the axillary bud (narrow black lines) and adventitious roots from sympodia I and V.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OTHER *CALLISTOPHYTON*-LIKE PLANTS

Several plants from Pennsylvanian sediments of North America and Permo-Carboniferous strata of France have a vegetative structure that compares closely with that of *Callistophyton*. None of these, however, has ever been examined with regard to possible taxonomic relationships to the Callistophytaceae. Plants of this type include species of the genus *Poroxylon* Renault (1879b), *Calamopitys kansanum* Baxter and Roth (1953), and *Lyginopteris* sp. (Reed, 1926).

The Poroxylaceae

The family Poroxylaceae Renault (1879a) is represented by the single genus *Poroxylon* Renault (1879b). Specimens consist of stems with attached petioles, buds and branches, and associated roots. Simple, strap-shaped leaves are present in the same material, and have been assigned to the other *Poroxylon* remains by association and presumed anatomical similarity. On the basis of leaf morphology, the Poroxylaceae is currently recognized as a family of the Cordaitales. Nevertheless, the similarity of the other organs to the monostelic seed ferns has been recognized by several authors (Scott, 1900, 1923; Seward, 1917) and a close comparison to *Callistophyton* is reflected in the specific epithet of *C. poroxyloides* (Delevoryas and Morgan, 1954). It also has been suggested that if the presently recognized *Poroxylon* leaves are found to belong to another plant then *Poroxylon* and *Callistophyton* may have to be combined (Delevoryas, 1962).

There are currently three recognized species of *Poroxylon*. The type species *P. boyssetii* Renault (1879b) and *P. edwardsii* Renault (1880) are best known. A third species, *P. stephanense* Bertrand and Renault (1886a), is described in only one publication, and has not been figured. Two additional species *P. duchartrei* Renault (1879b) (=*Heterangium*) and *P. sutcliffii* Scott (1909) have been found to represent other kinds of plants and are not retained in the genus (Seward, 1917; Scott and Maslen, 1910). According to Renault (1879b, 1880) *Poroxylon boyssetii* and *P. edwardsii* occur at the same locality near Autun, France. The *Poroxylon* material investigated in this study is from Autun. Specimens are either labelled *Poroxylon edwardsii*, or merely *Poroxylon*. All these specimens are specifically equivalent. Additional information on the structure and anatomy of *P. boyssetii* and *P. edwardsii* is found in several publications where numerous photographs and line drawings are presented (Renault, 1879b, 1880, 1893; Bertrand and Renault, 1886b; Seward, 1917; Scott, 1923). As originally described these two species are extremely similar. They differ primarily in only one feature; the structure of the secondary phloem (Renault, 1880).

The *Porpxylon* material from Autun consists of stems, buds and branches, petioles and roots. In all aspects the features of these *Poroxylon* organs agree with those of *Callistophyton*. *Poroxylon* specimens also exhibit axillary branching like that of *Callistophyton* Comp. Fig. 10, 14, 17). Stems of *Poroxylon* are typically slender (up to 2.3 cm in diameter); often with distantly spaced and slightly swollen nodes. In section view the stem consists of a parenchymatous pith surrounded by a ring of primary bundles and secondary xylem (Fig. 45). The leaf traces consist of two adjacent primary bundles, and the primary xylem exhibits an exarch maturation as do the Middle Pennsylvanian specimens of *Callistophyton* (Fig. 39). The number and position of axial bundles as seen in transverse sections of both nodal and internodal levels are identical with those of *Callistophyton* (Comp. Fig. 44, 45, 47; Text Fig. 2). The phyllotaxy of *Poroxylon* has been examined and is interpreted as that which produces a 5/13 leaf arrangement (Bertrand and Renault, 1886b). The diagrams of these authors, however, reveal that wedges of secondary wood rather than primary bundles were used in the phyllotactic interpretation (Fig. 198-200 of Bertrand and Renault, 1886b). The number and disposition of primary bundles at both nodal and internodal levels is identical with that of *Callistophyton* (Text Fig. 2). Consequently, the branch specimens are reinterpreted as having a 2/5 phyllotactic arrangement.

Anatomically, the Autun *Poroxylon* specimens are similar to *Callistophyton poroxyloides*, and identical with the Middle Pennsylvanian specimens. The anatomical features of *Poroxylon* are figures (Fig. 66-72) for comparison with those of the Middle Pennsylvanian *Callistophyton* (Fig. 57-65) and *C. poroxyloides* (Fig. 50-56). As in the North American specimens, the primary bundles of *Poroxylon* have a strand of parenchyma with protoxylem elements positioned at its centripetal side (Fig. 39). Protoxylem elements exhibit wall thickening patterns of the spiral and scalariflorm type (Fig. 68). Metaxylem elements are positioned at the centripetal and lateral margins of the trace, indicating an exarch maturation pattern like that of the Middle Pennsylvanian *Callistophyton* specimens (Fig. 39). Metaxylem elements have either oval bordered pits, or reticulate wall thickenings (Fig. 68). The secondary xylem of *Poroxylon* consists of alternating files of radially aligned tracheids and xylem rays (Fig. 67). The tracheids are large and angular, with up to 6 rows of alternately placed bordered pits on the radial walls (Fig. 66, 70). The rays are very high (Fig. 66), and most often biseriate (Fig. 69). In radial sections the ray cells are rectangular like those described for *Callistophyton* (Comp. Fig. 50, 57, 66). The secondary phloem of *P. edwardsii* is identical with that of *Callistophyton*, with radial files of sieve cells and phloem parenchyma that alternate with phloem rays (Fig. 71). In a radial plane the sieve cells and phloem ray parenchyma cells alternate. The secondary phloem of *P. boyssetii* is less prominent than that of *P. edwardsii*, and radial alignment of the cells is not evident (Fig. 13). There is also only a small amount of secondary wood in *P. boyssetii* (Fig. 13).

The presumed specific differences between *P. boyssetii* and *P. edwardsii* are therefore equivalent to the developmental differences among the *Callistophyton* stems described earlier. In this regard, these two *Poroxylon* species may be regarded as younger (*P. boyssetii*) and older (*P. edwardsii*) parts of the same species, or plant.

In section view the petioles and roots of *Poroxylon* are identical with those of *Callistophyton* (Comp. Fig. 3, 4, 15, 16; and 2, 6, 9). In section view the petiole of *Poroxylon* consists of a slightly adaxially arched, band-shaped trace with an abaxially placed band of secondary wood (Fig. 15). The trace is surrounded by a broad zone of thin-walled cortical cells, and a narrower outer zone of cortex with longitudinally disposed sclerenchyma strands. Like those of *Callistophyton*, the roots of *Poroxylon* are diarch with a wide zone of secondary xylem, and a prominent ray opposite each protoxylem strand (Fig. 9). Secondary phloem and periderm are present at the outer margin of more mature roots (Fig. 9). Tetrarch roots have been reported for *Poroxylon*, but have not been found in attachment to the stems and have not been figured. Roots of this type have not been observed in this study, and may belong to some other type of plant.

The other *Poroxylon* species, *P. stephanense*, Bertrand and Renault (1886a) is from deposits near Grand Croix, and is described as differing from other *Poroxylon* specimens in only minor respects. These include larger leaf trace bundles, and more secondary wood in the petiole than was found in the previously described material. In *Callistophyton*, both these features are quite variable. This material may therefore be equivalent to the Autun species.

The isolated leaves that are attributed to *Poroxylon* are found in association with *P. stephanense* (Bertrand and Renault, 1886a). These leaves are described and figured by Renault (1893, Plate 75, Fig. 4-10). In section view, they are characterized by a band-shaped region of vascular tissue surrounded by a thick zone of parenchymatous cortex (Renault, 1893, Plate 75, Fig. 4-6, 8, 10). The ground tissue also exhibits longitudinally oriented hypodermal fibers below a uniseriate epidermis. In these respects this foliage agrees with the structure of *Poroxylon* petioles. Agreement with *Cordaites* leaves is, however, more pronounced. As in *Cordaites*, the foliar vascular tissue consists of several parallel bundles that are separated by cortical parenchyma (Renault, 1893, Plate 75, Fig. 4, 8). The trace of *Poroxylon* petioles consists of either a single bundle, or laterally adjacent strands (Fig. 15). A continuous band of secondary wood accompanies the trace of *Poroxylon*, while in the associated foliage and *Cordaites* leaves a separate patch of secondary wood accompanies each isolated bundle (Renault, 1893; Harms and Leisman, 1961). It may be noted that the epidermis of the associated foliage exhibits longitudinally oriented rows of stomata between the hypodermal fibers. This is a feature of *Cordaites* leaves (Good and

Taylor, 1970). Stomata have not been observed in the petioles of either *Poroxylon* or *Callistophyton*. The secondary tracheids of the foliage are quite narrow, with only 2 - 3 rows of pits on the radial walls. This type of secondary tracheid is typical of the secondary wood in stems and leaves of *Cordaites*. The secondary tracheids in the stems and petioles of *Poroxylon* are larger and exhibit 4 - 6 rows of pits on the radial walls. In addition, the glandular cavities present in the ground tissue of *Poroxylon* are absent from the foliage. The above features clearly indicate that the associated foliage does not belong to the *Poroxylon* remains. On the other hand, the isolated foliage does agree closely with features of typical *Cordaites* leaves. This similarity is most pronounced when a comparison is made with *Cordaites crassus* Renault (1879b). In transverse section specimens of *C. crassus* exhibit hypodermal fibers accompanying the veins (Harms and Leisman, 1961). Sclerenchyma strands of this type are also present in the previously presumed *Poroxylon* foliage (Renault, 1893). No bundle sheath is described for this foliage, but tissue described by Bertrand and Renault as a later cambial zone (Bertrand and Renault, 1886b; Renault, 1893) surrounds each bundle, and agrees with the structure of the bundle sheath in *C. crassus* (Harms and Leisman, 1961). Since secondary tracheids are not present in the laminar parts of *Cordaites* leaves and the ground tissue of the French foliage is quite thick, the foliage previously attributed to *Poroxylon* apparently represents the basal part of a *Cordaites* leaf; probably *C. crassus*. In this regard it is interesting to note that specimens of *C. crassus* were first described from material that yields the Autun *Poroxylon* remains (Renault, 1879b).

Calamopitys kansanum

Calamopitys kansanum Baxter and Roth (1953) is described from the Fleming Coal of southeastern Kansas. It occurs in the same material as some of the Middle Pennsylvanian *Callistophyton* specimens (Baxter and Roth, 1953). This species is represented by a single specimen that consists of a short section of stem (Baxter and Roth, 1953).

The preserved stem section represents an area located just below a node, where a leaf trace ("reparatory strand" of Baxter and Roth, 1953) is separating from the stele (Fig. 7). The specimen is identical in all respects with smaller Middle Pennsylvanian *Callistophyton* stems from Illinois, Kentucky and Kansas. It consists of a parenchymatous pith surrounded by 9 primary bundles and the leaf trace (Fig. 46). No secondary wood accompanies the trace in this specimen. Several rows of radially aligned tracheids and xylem rays surround the pith area. The cambium, phloem and inner primary cortex are crushed and poorly preserved. A narrow zone of sclerenchymatous primary cortex forms the outer margin of the stem. A single outward projection from the cortex (Fig. 7, at arrow) is preserved in this specimen, and conforms to the structure of the cortical appendages of the other Middle Pennsylvanian *Callistophyton* specimens.

Lyginopteris sp.

A small apparently decorticated stem fragment from Upper Pennsylvanian deposits of Illinois has been tentatively identified as *Lyginopteris* sp. (Reed, 1926). The specimen measures 4 mm in diameter, and consists of a parenchymatous pith surrounded by primary xylem bundles and secondary wood. Maturation of the primary xylem is mesarch, and the primary bundles are directly adjacent to one another as in *Callistophyton poroxyloides*. The stem fragment exhibits a continuous zone of secondary wood around the pith area as in an internodal section of *C. poroxyloides*. Since the specimen is from deposits that are stratigraphically and geographically equivalent to those that bear *C. poroxyloides* it may be regarded as a poorly preserved specimen of the latter.

TAXONOMIC CONCLUSIONS

From the preceeding comparisons it is clear that the plants previously described as *Poroxylon boyssetii*, *P. edwardsii*, *Calamopitys kansanum* and *Lyginopteris* sp. (Reed, 1926) are generically equivalent to specimens of *Callistophyton*. Ordinarily *Poroxylon* Renault (1879b) would have priority and *Callistophyton* Delevoryas and Morgan (1954) would be regarded as a synonym. In this instance, however, the generic name *Poroxylon* was first used for a fossil coniferous wood fragment from the Tertiary of Germany (Andráe, 1850). *Poroxylon* Renault must therefore be regarded as a later homonym of *Poroxylon* Andrae, and *Callistophyton* Delevoryas and Morgan (being the ranking synonym) becomes the valid generic name. *Callistophyton poroxyloides* Delevoryas and Morgan (1954) may be regarded as the type species, with *Lyginopteris* sp. (Reed, 1926) being a specimen of the species. The Middle Pennsylvanian *Callistophyton* material, together with specimens previously described as *Poroxylon boyssetii*, *P. edwardsii* and *Calamopitys kansanum* represent a second species of *Callistophyton*. Among the names used for this species *Poroxylon boyssetii* Renault (1879b) has priority. The species is therefore designated as the new combination, *Callistophyton boyssetii*.

Material described as *Poroxylon stephanense* Bertrand and Renault (1886a) from Stephanien age deposits of France may represent additional material of *Callistophyton boyssetii*. At present, however, it is so poorly known that *Poroxylon stephanense* must be regarded as a dubious species until such a time as the original material becomes available for re-examination.

SYSTEMATIC SECTION

CLASS: PTERIDOSPERMOPSIDA Oliver and Scott, 1904.

FAMILY: CALLISTOPHYTACEAE Stidd and Hall, 1970b.

CALLISTOPHYTON Delevoryas and Morgan, 1954. Diagnosis emend.--Plants with slender stems, producing pinnately compound fronds and axillary buds or branches at each node. Adventitious roots present at some nodes. Stems measure up to 3 cm in diameter, constructed of central pith surrounded by primary xylem bundles. Bundles number 9 - 13 in section view, consist of 5 axial bundles and leaf traces. Leaf traces double stranded at leaf base. Cortex composed of thick parenchymatous inner zone, and outer zone with hypodermal fibers. Secondary tissues well developed in older stems; absent from stem, branch and bud apices. Secondary xylem of large tracheids, rays 1 - 5 cells wide. Distinct vascular cambium with fusiform and ray initials. Secondary phloem of rays alternating with radial files of sieve cells and phloem parenchyma. Periderm typically 2 - 5 layers of radially aligned cells; thick zone of randomly arranged cells in largest specimens. Ovoid-spherical secretory cavities with epithelial lining and occasional amber-colored contents present in primary ground tissue of all plant organs. Leaves typically bi- to quadripinnately compound with occasional dichotomous branching of petiole. Leaves at base of buds and branches simple, scale-like. Rachis and pinnae traces band-shaped in transverse sections. Continuous band of secondary wood accompanies petiole trace in some specimens. Pinnules with lobed margin; constricted at base. Ultimate veins branch dichotomously. Roots diarch. Secondary vascular tissue like that of stem; a prominent ray opposite each protoxylem strand. Periderm of radially aligned cells. Pollen organs abaxially borne on laminar fronds; synangiate with monosaccate, sulcate pollen. Ovules bilateral with free nucellus; vascularized by two integumentary strands and basal nucellar disc. Ovule attachment unknown.

Type species: *Callistophyton poroxyloides* Delevoryas and Morgan, 1954.

SYNONYMY

1879 *Poroxylon* Renault. Structure Comparée de Quelques Tiges de la Flore Carbonifère. Nouvelles Archieves du Muséum d'Histoire Naturelle. Tome deuxieme. Libraire de l'Académie de médecine, Paris. p. 272. (*non Poroxylon* Andrae, 1850).

CALLISTOPHYTON POROXYLOIDES Delevoryas and Morgan, 1954. Diagnosis emend.--Characteristics of species those of genus. Primary xylem development mesarch. Cortical appendages having constricted base and inflated tip;

apparently grandular. Secondary tracheids with up to 7 rows of bordered pits on radial walls.

Collecting localities: Berryville, Calhoun, New Calhoun,
Dix, Illinois.

Age: Upper Pennsylvanian.

SYNONYMY

1926. *Lyginopteris* sp. Reed. Flora of an Illinois coal ball. Bot. Gaz. 81: 466-467. Fig. 14.

*Callistophyton boyssetii** (Renault) Rothwell comb. nov.

Diagnosis--Characteristics of species those of genus. Primary xylem development exarch. Cortical appendages spine-like, having broad base of large cells and tapering to pointed apex of small, thick-walled cells. Secondary tracheids having up to 6 rows of bordered pits on radial walls.

Collecting localities: Sahara, Pit #11, Illinois; West
Mineral, Kansas; Providence,
Kentucky; Autun, France.

Age: Middle Pennsylvanian, North America. Upper Carboniferous (Lower Permian?), France.

Basionym: *Poroxylon boysseti* Renault (1879b).

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* To be validated later by publication.

SYNONYMY

1879. *Poroxylon boyssetii*. Renault. Structure Compareé de Quelques Tiges de la Flore Carbonifère. Nouvelles Archives du Museum d'Historie Naturelle. Tome deuxieme. Libraire de l'Académie de médecine, Paris. 273-276, Pl. 13 Fig. 5-13.

1880. *Poroxylon edwardsii*. Renault. Sur une nouvelle espece de *Poroxylon*. Compte Rendu des Séances de L'académie des Sciences. 91: 860-861.

1953. *Calamopitys kansanum*. Baxter and Roth. The coal-age flora of Kansas. IV. *Calamopitys kansanum*, a new species from the Pennsylvanian of Kansas. Trans. Kansas Acad. Sci. 56: 220-226.

DISCUSSION

Relationship of Vegetative Organs

The vegetative features of *Callistophyton* may be favorably compared to those of several other Paleozoic plants. The most striking similarities are with other monostelic seed ferns, but common features can also be found with the "polystelic" pteridosperms and cordaitaleans. The apparently scrambling and shrubby habit of *Callistophyton* (Text Fig. 1) is comparable to that proposed for the monostelic seed fern, *Lyginopteris* Potonié (1897) (Scott, 1923). Stems with a small diameter and little or no reduction in size toward the distal end suggest that several other members of the monostelic Lyginopteridaceae and Calamopityaceae may have had a similar habit. Plants of this type include *Heterangium* Corda (1845), *Rhetinangium* Gordon (1912), *Schopfiastrum* Andrews (1945), *Calamopitys* Unger (1856), and *Stenomyelon* Kidston and Gwynne-Vaughan (1912). Many other Paleozoic seed plants have a much larger stem diameter and apparently more upright or arborescent habit. These include the monostelic seed fern *Pitus* Witham (1833), the "polystelic" seed ferns *Medullosa* Cotta (1832) and *Sutcliffia* Scott (1906), and the cordaitalean genera *Cordaites* Unger (1850) and *Mesoxylon* Scott and Maslen (1910). Fern-like leaves and adventitious root production are characteristic of *Callistophyton* and several other seed ferns (*i.e. Lyginopteris, Heterangium, Medullosa*), but are not typical of the Cordaitales. On the other hand, axillary branching is a feature of *Cordaites* and *Mesoxylon* as well as *Callistophyton* and *Lyginopteris*.

In section view the stems of *Callistophyton* are constructed of a parenchymatous pith surrounded by a ring of primary bundles. The stele is enclosed by a broad zone of primary cortex. The secondary wood consists of large tracheids with prominent, typically biseriate rays. A definite vascular cambium with distinct fusiform and ray initials and abundant secondary phloem are found in well-preserved, older stems. All these features compare favorably with those of *Lyginopteris* and are quite similar to those of *Calamopitys*. Some species of *Calamopitys*, however, have more compact secondary wood with smaller tracheids and rays, and more massive primary xylem strands with a less well developed pith. In *Pitus* the tracheids and many of the rays are much smaller than those of *Callistophyton*. Other rays are up to 8 cells wide, but only a few cells in height. Several other monostelic seed ferns (*i.e. Heterangium, Rhetinangium, Schopfiastrum*) have secondary wood and other anatomical features like those of *Callistophyton*, but are characteristically protostelic. Stems of *Medullosa* and *Sutcliffia* are also anatomically similar to *Callistophyton*, but are protostelic and appear in transverse sections to have either two or more steles, or one main stele surrounded by subsidiary steles. The vascular cambium of *Medullosa* is indistinct with no clear differentiation of fusiform and ray initials, while that of *Sutcliffia* is unknown. Other anatomical features such as resin canals or resin cavities are found in the lyginopterid and medullosan pteridosperms as well as *Callistophyton*, but are characteristically absent from the cordaitaleans. Cortical appendages in the form of capitate glands are found in both *Callistophyton poroxyloides* and *Lyginopteris*. The stem structure of *Cordaites* and *Mesoxylon* is similar to *Callistophyton*, but the secondary wood is much less compact in the latter. The pith of the cordaiteans is also distinct, with the tissue restricted to septa rather than uniformly parenchymatous as in *Callistophyton*. The primary cortex of most Paleozoic seed plants is constructed of an inner parenchymatous zone and an outer zone with longitudinally oriented hypodermal fibers. This structure is found in the monostelic seed ferns, the "polystelic" seed ferns, and the cordaiteans as well as *Callistophyton*. In *Lyginopteris* and *Pitus* the fibers anastomose frequently, forming what appears as a meshwork in tangential sections. In the other forms this feature is not apparent.

Of those Paleozoic seed plants with a well developed pith surrounded by primary bundles, the primary vascular structure of *Callistophyton* is most similar to that of *Lyginopteris*. In both genera there are five independent axial bundles that produce leaf traces in a 2/5 phyllotactic spiral. The leaf traces of both divide and are double stranded at the level of the leaf base. Several species of *Stenomyelon* and *Calamopitys* also exhibit a 2/5 phyllotaxy, but are either protostelic or have interconnected axial bundles (Beck, 1970). One exception is *Calamopitys foerstei*, where the interconnections are incomplete (Beck, 1970). Transverse sections of the primary xylem of *Pitus*, *Cordaites* and *Mesoxylon* appear similar to those of *Callistophyton*. In the former genera, however, there are a much larger number of primary bundles, and presumably a more complex phyllotactic spiral. The courses of the axial bundles have not been determined in *Pitus* or the cordaitean genera, but the leaf traces are known to divide more than once while in the stem. Consequently, there are 3 - 6 traces in the leaf base of *Pitus* (Long, 1963) and 4 - 8 traces at comparable levels of *Cordaites* and *Mesoxylon*.

The leaves of *Callistophyton* are most like those of the lyginopterid pteridosperms. Individual leaves are pinnately dissected fern-like fronds, and would be referrable to *Sphenopteris* or *Mariopteris* if found in the compressed state. Dichotomous branching of the rachis is characteristic of lyginopterid seed ferns, but occurs only rarely in *Callistophyton*. Internally, *Callistophyton* fronds and those of *Lyginopteris*, *Rhetinangium*, and *Schopfiastrum* have massive petiole traces, but the trace of *Callistophyton* is collateral, while the others are probably concentric. In *Heterangium* and in the Calamopityaceae (*e.g. Kalymna*) several smaller traces are typically present in the petiole. The leaves of the medullosan pteridosperms are also pinnately dissected fern-like fronds with a dichotomously branching rachis, but are typically quite large and of the *Neuropteris* or *Alethopteris* compression types. Internally, the rachis is characterized by a large number of small traces. The fronds of *Pitus* (*e.g. Lyginorachis papilio*, Long, 1963) have an overall structure like those of the Lyginopteridaceae, but the pinnule configuration is unknown. Above the most proximal levels there is one massive trace, but the bundle is probably concentric. The leaves of *Cordaites* and *Mesoxylon* are unlike those of either *Callistophyton* or any other known Paleozoic pteridosperm. Individual cordaitean leaves are simple strap-shaped structures with a smooth, entire margin. Internally there are a large number of small, collateral bundles present in transverse sections.

The roots of *Callistophyton* are diarch with no primary xylem parenchyma. Those of *Lyginopteris* have 4 - 8 protoxylem strands and a large amount of parenchyma at the center of the stele. The roots of *Heterangium* are more like those of *Callistophyton*, with 2 - 3 protoxylem strands, and broad rays in the secondary wood opposite the protoxylems. The structure of the roots of *Rhetinangium* and *Schopfiastrum* are unknown. The roots of *Medullosa* have a variable number of protoxylem strands, with 3 (*M. anglica*, Scott, 1899) or 4 (Hoskins, 1931) being the most common.

The roots of cordaitean plants (*e.g. Amyelon*) are also characterized by a variable number of protoxylem strands. Some have primary xylem composed entirely of tracheids, but others have a prominent zone of thin-walled cells at the center of the stele. The secondary wood of these latter roots is comparable to that of the stems, and is, therefore, much more compact than the wood of *Callistophyton* roots.

Among presently recognized forms of Paleozoic gymnosperms the vegetative features of *Callistophyton* compare most closely to those of other monostelic seed ferns, and particularly those of *Lyginopteris*. The overall habit as well as the structure and anatomy of the stems and leaves are remarkably similar in *Callistophyton* and *Lyginopteris*. Even the primary vascular system and branching pattern are the same. One can easily understand why *Callistophyton* was originally assigned to the Lyginopteridaceae. Indeed, if the fertile parts of *Lyginopteris* and *Callistophyton* were unknown, one would be inclined to regard them as two very closely related genera. Examination of the fertile structures of *Callistophyton*, however, reveals that they are totally unlike those of the Lyginopteridaceae, and also unlike those of any other previously described, structurally preserved pteridosperm.

Relationship of Reproductive Structures

Prior to the recognition of the fertile structures of

Text Fig. 5. Reproductive structures of Paleozoic gymnosperms. The figures from top to bottom are mid-longitudinal and mid-transverse section views of ovules, mid-longitudinal and mid-transverse section views of pollen producing structures, and pollen grains with the proximal surface oriented upward. Figures are not to scale. Vascular tissue is represented by dashed lines in the longitudinal sections, and by large black dots in the transverse sections. In the ovules the stippled areas represent integument, and the inner lines represent nucellus and pollen chamber. The nucellus is included only where it is separated from the integument. In the pollen producing structures the stippled areas represent ground tissue. Stippled areas of the pollen grains represent bladders. The arrows above the grains indicate proximal (upward) or distal (downward) germination of the grains.

The structures from left to right are those of cordaites and conifers (under C - C); those of the Callistophytaceae (under C); those of monostelic seed ferns in the Lyginopteridaceae, Calamopityaceae and *Pitus* (under M); and those of the polystelic seed ferns (under P).

Fig. 5a. *Cardiocarpus*.

Fig. 5b. *Callospermarion pusillum*.

Fig. 5c. *Conostoma*.

Fig. 5d. *Pachytesta* (redrawn from Taylor, 1965).

Fig. 5e. *Cordaianthus* fertile scale (redrawn from Florin, 1951).

Fig. 5f. *Idanothekion glandulosum*.

Fig. 5g. *Telangium scotti* (drawn after description of Benson, 1904).

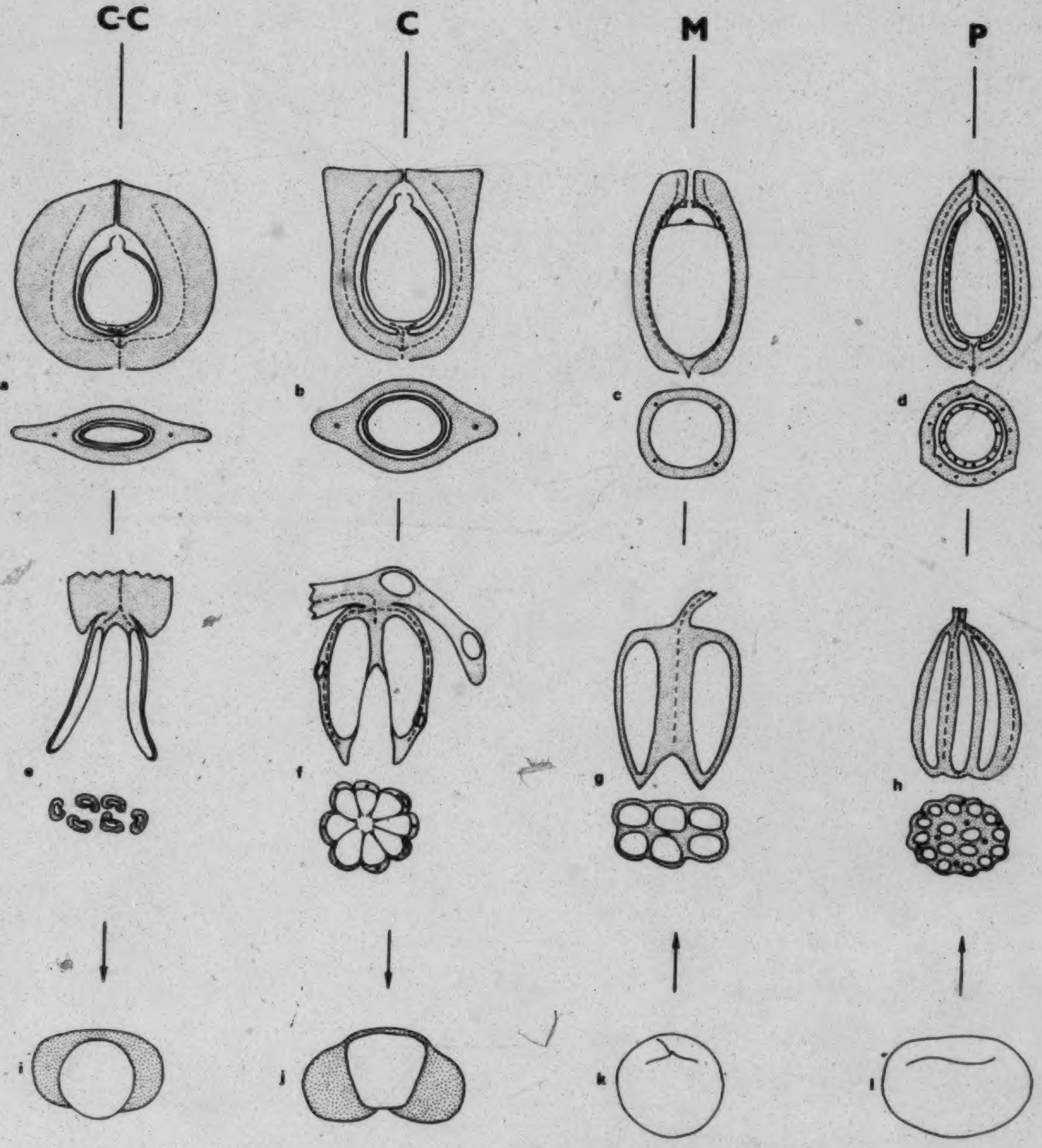
Fig. 5h. *Heterotheca grievii* (redrawn from Schopf, 1948).

Fig. 5i. *Florinites* (redrawn from Schopf, Wilson and Bentall, 1944).

Fig. 5j. *Vesicaspora* (redrawn from Millay and Eggert, 1970).

Fig. 5k. Spherical or ovoid, and trilete prepollen grain.

Fig. 5l. Oblong, monolete prepollen grain.


C-C
C
M
P
a
b
c
d
e
f
g
h
i
j
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l

Callistophyton the reproductive organs of structurally preserved Paleozoic gymnosperms could be placed in three general categories. These include the structures associated with the monostelic seed ferns, those associated with the "polystelic" seed ferns, and those belonging to cordaites and conifers. The structure of these organs together with those of *Callistophyton* are presented in Text Fig. 5. Ovules, pollen bearing structures, and pollen grains are included so that comparisons can be made between the groups. A fourth feature, position of the ovules and pollen bearing structures, cannot be conveniently figured, but is included in the following discussion.

Based on structure, isolated Paleozoic ovules have been placed in three form orders; the Trigonocarpales, the Lagenostomales, and the Cardiocarpales (Seward, 1917). Among structurally preserved Paleozoic remains the Trigonocarpales are generally assigned to the medullosan pteridosperms, while the Lagenostomales are assignable to the monostelic seed ferns (*i.e.* Lyginopteridaceae, Calamopityaceae, *Pitus*). Structurally preserved specimens assignable to the Cardiocarpales are traditionally assignable to Paleozoic cordaites and conifers. The discovery of similar compression forms in attachment to (Grand'Eury, 1905; Seward, 1917; White, 1904; Cridland and Morris, 1960) or close association with (*i.e.* Delevoryas and Taylor, 1969) pteridospermous type foliage, however, suggests their production by seed ferns as well. Specimens of the

Trigonocarpales are radially symmetrical and typically three-angled in transverse sections. The nucellus is attached to the integument at the base and free at more distal levels. The pollen chamber is of a relatively simple type with an undifferentiated wall and usually no organized floor. Vascular tissue is present in the sarcotesta (outer soft layer) of the integument, and in the nucellus from the base to the level of the base of the pollen chamber. Petrified ovules have not been found in attachment to vegetative structures, but compression specimens are known to have been borne on foliar fronds (Halle, 1933). Lagenostomalean ovules are typically radially symmetrical, but some platyspermic forms are also known. The nucellus is typically attached to the integument at the base and at the sides up to the level of the pollen chamber. The pollen chamber is a relatively complex structure, with an organized floor region and a pollen chamber wall with a typically specialized apex (Rothwell, 1971). The vascular tissue is located in the endotesta (inner soft layer) of the integument only. No tracheids are present in the nucellus. Lagenostomalean ovules are known to have been loosely enclosed in a structure referred to as a cupule. As originally defined, this group of ovules was thought to have been borne on the foliar fronds of lyginopterid pteridosperms. More recently, however, ovules of this type (Sporne, 1965) have also been found in association with the Calamopityaceae and *Pitus* (Long, 1963), and compression specimens indicate an attachment to the probable fronds of *Pitus* (Long, 1963). Until recently, petrified specimens of the Cardiocarpales were regarded as ovules of the Cordaitales or Coniferales. Specimens of this type are bilaterally symmetrical and flattened. The nucellus is attached to the integument at the base and free above as in the Trigonocarpales. The pollen chamber is also like that of the latter group, with an undifferentiated wall and no organized floor region. Vascular tissue is present in the sarcotesta of the integument, where it usually consists of two vascular strands. Tracheids are also present in the nucellus, but unlike specimens of the Trigonocarpales, are restricted to the base. Unlike the previously described ovule types, specimens assignable to the cordaites and conifers are born in compound cones or strobili (Florin, 1951). More recently, some small ovules of this type have been suggested as having pteridospermous affinities (*e.g. Taxospermum undulatum* Neely, 1951; *Callospermarion pusillum* Eggert and Delevoryas, 1960), and *Callospermarion* has been proposed as the ovule of *Callistophyton poroxyloides* (Stidd and Hall, 1970b). Although *Callospermarion* agrees with all the structural features of the other members of the Cardiocarpales, it is not known to have been borne in a cone. The only evidence of the attachment of this ovule is that of Stidd and Hall (1970a), where a single specimen is described in attachment to a stalk-like structure. Unfortunately, the stalk-like structure is not attached, and it is also not recognizable as any previously described structure that is assignable to *Callistophyton poroxyloides*. Nevertheless, the association of the ovules with the vegetative remains together with anatomical similarities (*i.e.* presence of secretory cavities in the integument of *Callospermarion*) and the presence of *Callistophyton*-type pollen (*i.e. Vesicaspora*) in the pollen chamber, strongly suggests that the interpretation is correct. In this regard, one can consider *Callistophyton* to have produced ovules that are unlike those known for any previously described, structurally preserved, Paleozoic pteridosperm. While at the same time, these ovules are essentially the same as those produced by Paleozoic cordaites and conifers.

The pollen producing structures of the "polystelic" seed ferns, the monostelic seed ferns, and *Callistophyton* are all referred to as pollen organs, and were all presumably born on foliar fronds. The structure of the pollen organs and the mode of attachment to the frond are, however, distinct in each group. The pollen producing structures of Paleozoic cordaites and conifers were stobili or cones. In the conifers the cones were simple, while in the cordaites the cones were compound (Florin, 1951).

Petrified pollen organs of the polystelic seed ferns (*e.g. Dolerotheca* Halle, 1933; *Rhetinotheca* Leisman and Peters, 1970; *Halletheca* Taylor, 1971) consist of large, tubular sporangia that are fused into a synangium. The sporangia are often imbedded in parenchymatous, or parenchymatous and sclerenchymatous ground tissue. Sporangial dehiscence is either terminal (*i.e. Dolerotheca* Schopf, 1948), or there is no evidence of a specialized dehiscence mechanism (*i.e. Rhetinotheca* Leisman and Peters, 1970; *Halletheca* Taylor, 1971). These pollen organs are relatively large; typically measuring over one centimeter long. Of the above forms only *Dolerotheca* has had its position on the plant determined (Ramanujam and Stewart, in press). This pollen organ is attached to a medullosan frond with *Myeloxylon*-type pinnae anatomy, and *Alethopteris*-type pinnules. The pollen organs are found in the position that would normally be occupied by a penultimate pinna and its attached pinnules. The pollen organs of the monostelic seed ferns (*e.g. Crossotheca* Zeiller, 1883; *Telangium* Benson, 1904; *Telangiopsis* Eggert and Taylor, 1971) are typically smaller than those of the medullosans; often measuring only about 1 - 5 mm long. Individual pollen organs are constructed of several sporangia that are fused at the base or fused to a basal stalk. The sporangia are either arranged in a ring, or in two parallel rows, and some may have been bilocular (Scott, 1923; Eggert and Taylor, 1971). The sporangia are elongate structures that either show evidence of longitudinal dehiscence (*e.g. Telangiopsis*) or no dehiscence mechanism. Pollen organs are borne on the terminal segments of fronds, or parts of fronds, without laminar pinnules. The pollen cones of the cordaites (*e.g.*

Cordaianthus Grand-Eury, 1877) are constructed of a central axis that bears secondary axes in the axils of bracts (Florin, 1951). The secondary axes bear spirally arranged appendages referred to as scales (Florin, 1951). Some of the more terminal scales are fertile and bear at their tips 2 - 6 sporangia. The sporangia are elongate and arranged in a ring, and are fused at the base. Individual sporangia dehisce by a longitudinal slit located in the inwardly directed sporangial wall. A single vascular bundle from the tip of the scale divides producing a vascular strand that enters the base of each sporangium. The pollen organs of *Callistophyton* (*e.g. Idanothekion* Millay and Eggert, 1970; *Callandrium* Stidd and Hall, 1970a) are constructed of a ring of elongate sporangia that are laterally fused to near their distal ends. Proximally, the sporangia surround a column of tissue known as the central column, and distally they surround a hollow. Dehiscence is by a longitudinal slit located on the inwardly directed wall as in *Cordaianthus* sporangia. The pollen organs are borne on the abaxial surface of apparently unmodified *Callistophyton* pinnules (Stidd and Hall, 1970a; Rothwell, 1972b). A single vascular bundle of the pinnule bends abaxially and enters the central column of each pollen organ. In *Idanothekion* a single vascular strand extends from the central column region, into each sporangium.

At first glance, the pollen organs of *Callistophyton* appear more like those of other pteridosperms than the pollen producing structures of the cordaites. The relatively unfused, bilocular sporangia of *Crossotheca*, and the large, tubular sporangia of medullosan pollen organs that are imbedded in ground tissue are, however, quite distinct from *Callistophyton* pollen organs. If one compares the structure of the sporangia at the tip of a fertile *Cordaianthus* scale to a *Callistophyton* pollen organ, several similarities can be seen. In both cases the sporangia are elongate structures that are arranged in a ring. The sporangia of both dehisce by a longitudinal slit located on the inwardly directed wall. In *Cordaianthus* the sporangia are fused at only the base, while the *Callistophyton* pollen organs are laterally fused to near the tips, and proximally surround a central column. In both *Cordaianthus* and *Idanothekion* there is a vascular strand that enters each sporangium. In the former, however, the strand is present at only the base, while in the latter the strands extend to near the sporangial tips. Vascular tissue is absent from the sporangia of *Callandrium*. There is also no vascular tissue at the base of the *Cordaianthus* sporangia that is comparable to the vascularized central column of the *Callistophyton* pollen organs. An additional distinction between the pollen organs of *Callistophyton* and the sporangia of *Cordaianthus* is the position of attachment. In *Callistophyton* the pollen organs are borne on the abaxial surface of a laminar pinnule, while the sporangia of *Cordaianthus* are terminally placed.

The pollen of *Callistophyton* and Paleozoic conifers and cordaites is constructed of a central body surrounded by an ovoid or bilobed air bladder or saccus. The saccus is typically ornamented by an internal reticulum. Germination of these pollen grains is considered to be distal as in living conifers. Some cordaite or conifer grains exhibit a trilete suture on the proximal surface. This feature is absent from others, and also *Callistophyton* grains. One other distinction of *Callistophyton* grains is the presence of a distal sulcus or germinal furrow. This feature is present in more recent fossil and extant bisaccate conifer grains but is absent from *Florinites* grains. The grains of the polystelic- and monostelic seed ferns can be easily distinguished from those discussed above. Grains of this type are considered to have proximal germination, and are therefore referred to as prepollen (Schopf, 1938). Grains of the monostelic seed ferns are typically spherical or ovoid with a trilete suture. Prepollen of medullosan pteridosperms is characteristically oblong in shape with a monolete suture (Text Fig. 5).

Phylogenetic Significance of the Callistophytaceae

Much of our present understanding of the evolution of gymnosperms is derived from studies of the late nineteenth and early twentieth centuries (Arnold, 1948; Chamberlain, 1935). Workers of the time were impressed by the distinctive characteristics of the two most prominent groups of extant gymnosperms; conifers and cycads. Known fossil evidence of the time suggested that each group could be traced as far back as evidence could be found. These ideas were probably most concisely stated by Chamberlain (1935) in the recognition of two separate lines of gymnospermous plants; the coniferophytes and the cycadophytes. Taxa that are included among the coniferophytes include the Cordaitales, Coniferales, Ginkgoales, and Gnetales (Chamberlain, 1935). The coniferophytes are characterized as large, profusely branched plants with simple leaves. In section view the stems have a small pith, abundant wood and scanty cortex. The reproductive structures are borne in strobili or cones. The pollen cones are either simple or compound, but the ovulate cones are characteristically compound. According to Chamberlain (1935) the cycadophytes are represented by the Cycadofilicales (=Pteridospermales), Bennettitales (=Cycadeoidales), and Cycadales. This group is characterized by usually small, unbranched plants with pinnate leaves. In section view the stems have a large pith, scanty wood and thick cortex. The reproductive structures are borne on leaves or leaf-like organs. In the Cycadeoidales and Cycadales the ovulate reproductive structures are interpreted as being aggregated into simple cones (Chamberlain, 1935). Among extant gymnosperms, the cycads and conifers can be further divided by the structure of the male gametophytes and the behavior of the male gametes. In conifers the pollen produces a pollen tube that carries the nonmotile sperm to the egg. In the cycads the pollen tube is apparently only an haustorial structure. The pollen produces motile, ciliated gametes that are released in the pollen chamber and swim to the egg.

As a member of the Pteridospermales, the Callistophytaceae may be regarded as a family of cycadophytes. In respect to the above features, the vegetative organs of *Callistophyton* compare favorably with the structure of a typical cycadophyte. The plants are relatively small and have pinnately compound leaves. In young stems the pith is relatively large and the cortex is quite thick. Other features, however, do not conform to the expected pteridosperm characteristics. These include the much-branched nature of the stems (*i.e.* an axillary bud or branch present at each node) and the large amount of secondary wood present in older stems. Like typical cycadophytes, the pollen producing organs of *Callistophyton* are borne on leaves. As yet it is not known how the female organs were borne. The reproductive organs themselves are unlike those of other presumed Paleozoic cycadophytes. On the contrary, they are very much like those of Paleozoic coniferophytes. These similarities are most striking in the structure of the ovules (compare *Cardiocarpus* and *Callospermarion* in Text Fig. 5) and the true pollen (compare *Florinites* and *Vesicaspora* in Text Fig. 5). Although less obvious, the structure and arrangement of

Callistophyton pollen organs and a group of cordaitean sporangia are quite similar (compare the fertile scale of *Cordaianthus* with *Idanothekion* in Text Fig. 5). They differ primarily in only the degree of sporangial fusion and the extent of vascularization. One additional similarity of *Callistophyton* and some coniferophytes is the structure of the male gametophyte. The pollen of *Callistophyton* is known to have produced a branched pollen tube that is comparable to the sperm carrying pollen tubes of some extant conifers (Rothwell, 1972a).

As with most ideas concerning the phylogeny of major plant groups, an ever increasing body of evidence relating to gymnospermous plants necessitates a constant reevaluation of the group. Some initially inherent problems with the "coniferophyte-cycadophyte" interpretation of gymnosperm phylogeny are found among the extant forms. The Gnetales are placed in the coniferophytes because their fertile parts are borne in compound strobili similar to those of the Cordaitales and Coniferales. Of the gnetalean genera, however, *Ephedra* and *Welwitschia* are small plants, and *Welwitschia* is virtually unbranched. In addition, ovules produced by members of the Gnetales exhibit a double integument, a feature known elsewhere in only the angiosperms. The leaves of *Ephedra* are small and scale-like as in some conifers, but those of *Gnetum* and *Welwitschia* are quite distinctive. The leaves of *Gnetum* have definite petiole and blade regions, and netted venation like those of typical dicotyledonous angiosperms. In *Welwitschia* only two leaves are produced by a plant, and these are large, persistent structures with a continuously active basal meristem.

Equally disturbing deviations from the coniferophyte concept are found in *Ginkgo*. The anatomical features of the stem and long shoots are like those of other coniferophytes, but the short shoots have a large pith, scanty wood, and thick cortex like that of typical cycadophytes. In addition, the ovules of *Ginkgo* are not borne in a well defined strobilus. On the contrary, evidence from abnormal ovulate structures suggests that the seeds are borne on modified leaves (Fujii, 1896). The microgametophytes of *Ginkgo* produce ciliated sperm like those of extant cycads, rather than having pollen-tube carried sperm as in conifers.

Problems with the coniferophyte-cycadophyte separation of gymnosperms are also apparent among fossil plants. *Pitus*, a Lower Carboniferous arborescent form with coniferophyte-type wood, was once thought to represent the oldest known coniferophyte (Arnold, 1948). More recently, however, this plant has been found to represent a pteridosperm with highly dissected leaves and reproductive organs like those of the Calamopityaceae and Lyginopteridaceae (Long, 1963). Consequently, by using evidence arising from both living and fossil forms it has become increasingly difficult to clearly distinguish between coniferophyte and cycadophyte plants. In light of this uncertainty, the significance of the Callistophytaceae can be more easily interpreted.

From a purely speculative point of view it would seem more logical that the gymnosperms evolved from a single pregymnospermous complex (Scheckler and Banks, 1971), rather than from two or more unrelated lines (Beck, 1971). Such an interpretation eliminates the necessity for parallel or convergent evolution to account for the general similarity in structure and function of the gymnospermous reproductive parts. This interpretation also accounts for the nearly simultaneous appearance in the Upper Devonian and lowermost Lower Carboniferous of what are now considered to be separate gymnospermous lines (Arnold, 1948). From this hypothetical early seed-plant complex one would expect to find evidence of rapid adaptive radiation producing numerous groups of seed plants that exhibit a multitude of possible character combinations. Examination of the characteristics of the presently known groups of upper Paleozoic and Mesozoic seed plants (*i.e.* Pituaceae, Long, 1963; Calamopityaceae, Lyginopteridaceae, Medullosaceae, Seward, 1917; Callistophytaceae, Stidd and Hall, 1970b; Cordaitaceae, Lebachiaceae, Voltziaceae, Florin, 1951; Caytoniaceae, Thomas, 1925; Corystospermaceae, Thomas, 1933; Peltaspermaceae, Harris, 1932; Pentoxylaceae, Sahni, 1948; Cycadeoidaceae, Williamsoniaceae, Wielandiellaceae, Sporne, 1965; Cycadaceae, Chamberlain, 1935) indicates that a large number of possible gymnospermous character combinations are indeed present in fossil representatives. With respect to these considerations, *Callistophyton* may be interpreted as representing one combination of gymnospermous characters that has no recognisable descendants among the extant flora.

If, on the other hand, seed ferns are interpreted as the precursors of several more recent and advanced groups (*e.g.* angiosperms), then characters such as fern-like foliage and leaf-borne reproductive organs may be considered primitive. If so, then the Callistophytaceae can also be interpreted as related to the Cordaitales and Coniferales. The structure of the ovules, pollen organs and pollen is evidence of this relationship. The primitive *Callistophyton* vegetative structures can be interpreted as reflecting the structure of cordaite and conifer ancestors. Indeed, the anatomy of the stems of some species of *Cordaites* and *Mesoxylon* do approach that found in pteridosperms such as *Schopfiastrum* and *Callistophyton* (Delevoryas and Morgan, 1954; Rothwell and Taylor, 1972; Scott, 1923). Even the large, entire-margined and strap-shaped leaves of *Cordaites* are not too far removed from the foliage of *Callistophyton*. This is evidenced by the occurrence of a gradation from highly dissected leaves (as in *Callistophyton*) to entire-margined and strap-shaped leaves (as in *Cordaites*) within the extant fern family Polypodiaceae. The simple, entire-margined leaves found at the base of buds and branches in *Callistophyton* may even foreshadow a tendency toward such a structure of the leaves.

The significance of the structures assignable to the Callistophytaceae are indeed puzzling. The numerous possible interpretations are unfortunately weakened by the absence of more precise and complete evidence of the earliest seed plants. The implications of the evidence provided by *Callistophyton* as it relates to currently accepted interpretations of gymnosperm phylogeny is much too obvious to be overlooked. From this evidence it is clear that one can no longer assume, *a priori*, the separation of gymnosperms into two distinct groups - coniferophytes and cycadophytes. The characteristics of the Callistophytaceae serve only to emphasize the fact that no clear cut distinction can be made between Cycadophytes and Coniferophytes at relatively early stages in gymnosperm evolution.

Figs. 1 - 9. Transverse sections of stems, petioles and roots to illustrate their general features for comparison of specimens from different localities. (lt=leaf trace, p=pith, pd=periderm, sx-secondary xylem).

Fig. 1 - 3. *Callistophyton poroxyloides.*

Fig. 1. Stem cross section at internodal level. C.B. 5,821 top A #15 X 6(CP-B-2).

Fig. 2. Large root specimen. Arrows indicate protoxylem. C.B. 3,791 $G_{(1)}$ top. #4 X 6(CP-B-8).

Fig. 3. Petiole near base. Note secondary xylem. C.B. 5,821 top A #10 X 12(CP-B-9).

Fig. 4 - 9. *Callistophyton boyssetii.*

Fig. 4. Petiole near base. Compare with Fig. 3. C.B. 3,259 G bot. #105 X 12(CB-S-1).

Fig. 5. Stem at similar level to Fig. 1. C.B. 5,754 H bot b. #26 X 6(CB-S-2).

Fig. 6. Mature root for comparison with Fig. 2. Arrows indicate protoxylem. C.B. 289 A bot. #77 X 10(CB-S-3).

Fig. 7. Stem at level similar to that of Fig. 1 and 3. Arrow indicates cortical appendage. (previously designated as *Calamopitys kansanum*). #1454 X 14(CB-W-4).

Fig. 8. Stem at level similar to Fig. 1, 3, and 7. (previously designated as *Poroxylon edwardsii*). #1,430 X 6(CB-A-5).

Fig. 9. Mature root for comparison with Fig. 2 and 6. Arrows indicate the position of the protoxylem strands. (originally designated as *Poroxylon* root). #1,428 X 27(CB-A-6).

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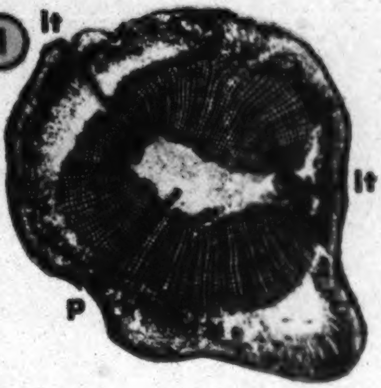

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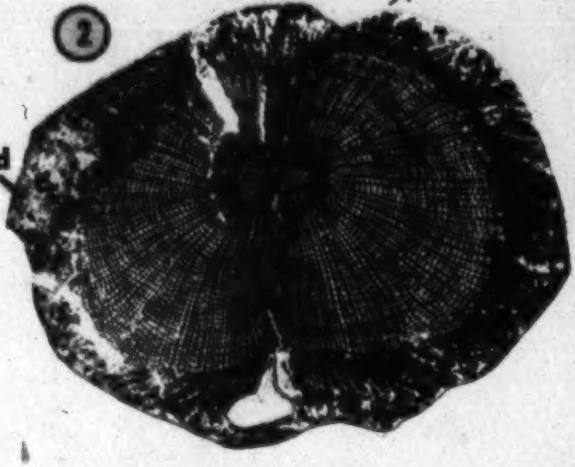

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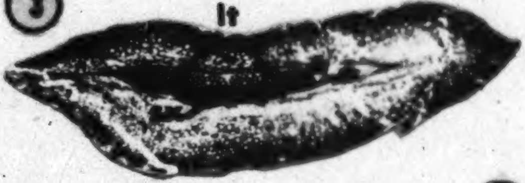

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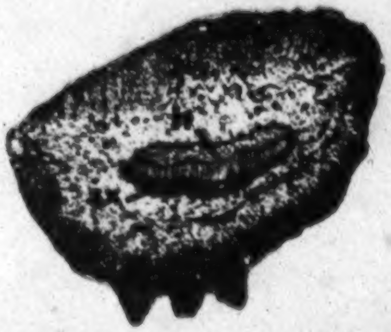

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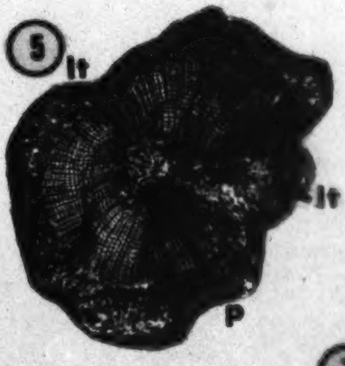

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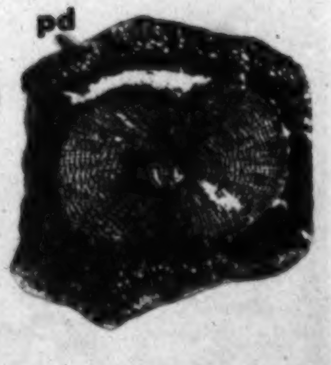

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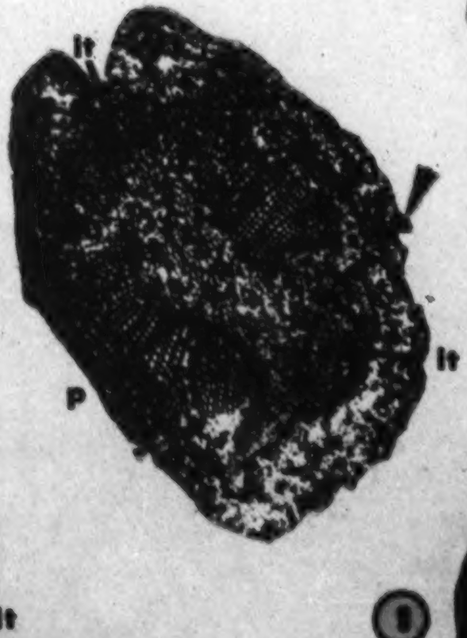

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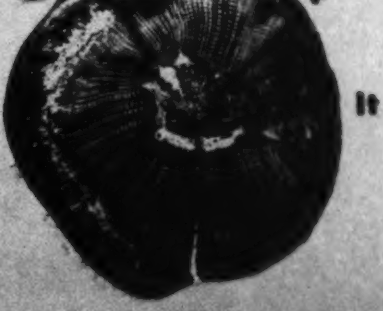

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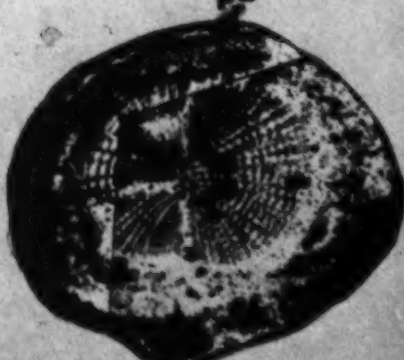

Figs. 10 - 18. Transverse sections of young stems, mature branching stems, and petioles. (br=branch, bu=bud, l=leaf, lt=leaf trace, p=pith, pc= procambium, sc=secretory cavity, sx=secondary xylem).

Fig. 10 - 12. *Callistophyton poroxyloides.*

Fig. 10. Large stem at nodal level. Note the position of the departing leaf, subsequent leaf trace and axillary bud. C.B. 1,221 I bot #23 X 6 (CP-B-1).

Fig. 11. Immature stem; section from near apical bud. #687 X 14(CP-B-6).

Fig. 12. Immature petiole. Compare with Fig. 3, 4, 15 and 16. #2,224 X 14(CP-B-7).

Fig. 13 - 18. *Callistophyton boyssetii.*

Fig. 13. Young stem. Compare with Fig. 11 and 18. (originally designated as *Poroxylon boyssetii*). Photograph taken from Renault, 1879b (Plate 13, Fig. 5).

Fig. 14. Large stem at nodal level. Compare with Fig. 10. (originally designated as *Poroxylon*). #2,964 X 6(CP-A-7).

Fig. 15. Petiole with secondary xylem. Compare with Fig. 3, 4, 12, and 16. (originally designated as *Poroxylon boyssetii*). Photograph taken from Renault, 1879b (Plate 13, Fig. 11).

Fig. 16. Large petiole with no secondary xylem. Compare with Fig. 3, 4, 12, and 15). O.U. C.B. #4,007 D bot #1 X 12 (CB-S-8).

Fig. 17. Large stem at nodal level. Compare with Fig. 10 and 14. C.B. #3,521 G top #88 X 6(CB-S-9).

Fig. 18. Young stem. Compare with Fig. 11 and 13. C.B. 3,521 A bot a #21 X 8(CB-S-10).

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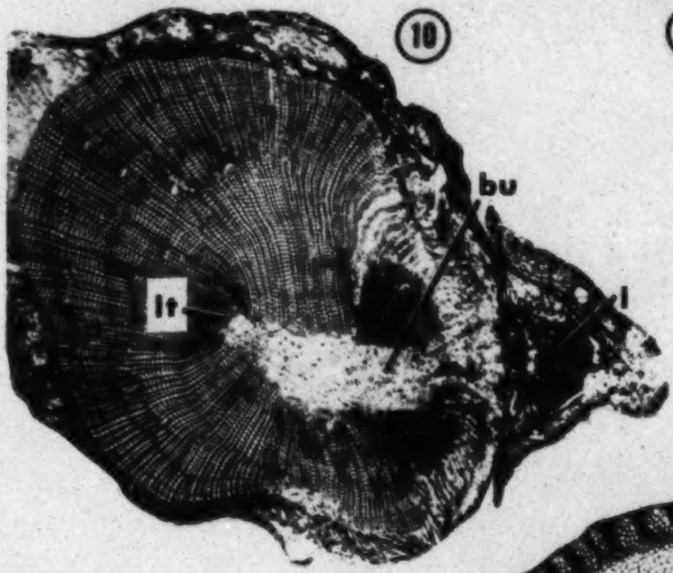

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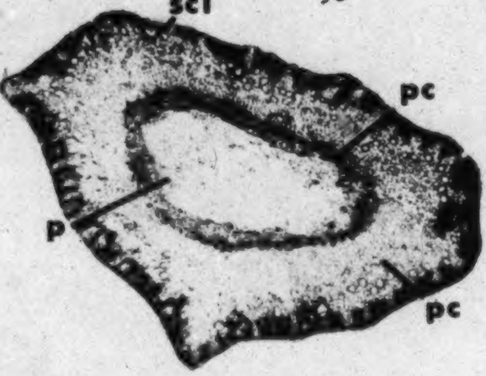

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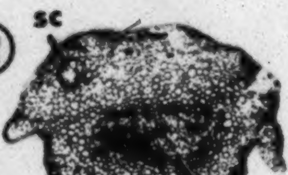

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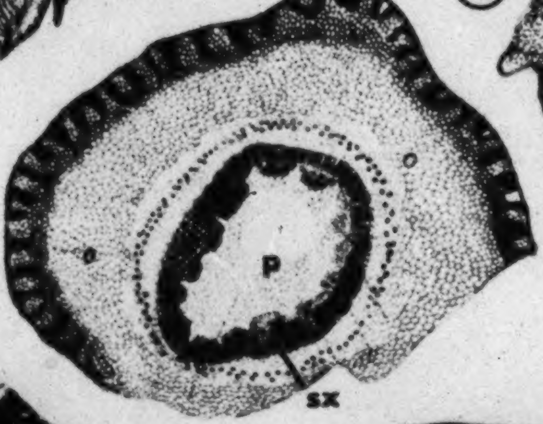

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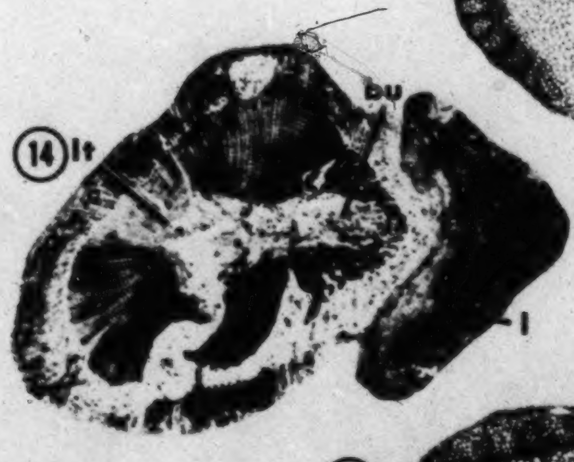

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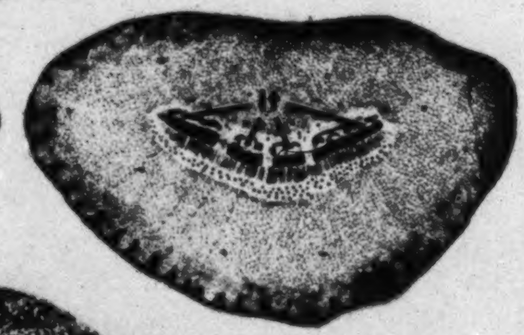

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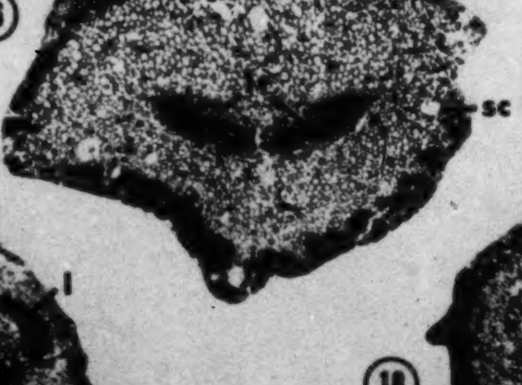

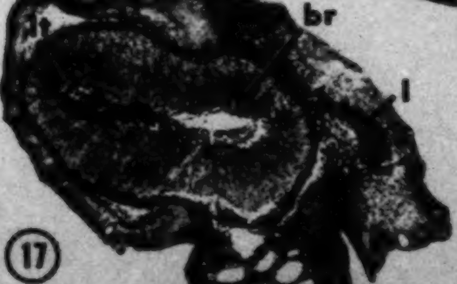

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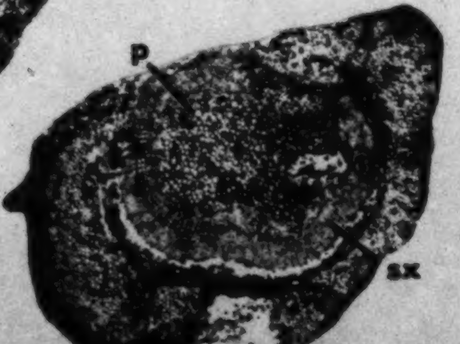

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Figs. 19 - 27. *Callistophyton poroxyloides*. (pa=parenchyma, pr=protoxylem, sc=secretory cavity, vb= vascular bundle).

Fig. 19 - 23. Transverse sections of stems with increasing amounts of secondary development. Note the increase in secondary xylem thickness, the decrease in cortex thickness, and the increasing periderm thickness from #19 to #23.

Fig. 19. C.B. 1,160D(1) bot #41 X 6(CP-B-6)

Fig. 20. C.B. 5,821 top A #15 X 6(CP-B-4)

Fig. 21. C.B. 5,821 top A #10 X 6(CP-B-3)

Fig. 22. C.B. 5,821 top A #15 X 6(CP-B-2)

Fig. 23. C.B. 5,821 top A #2 X 6(CP-B-1)

Fig. 24. Transverse section of sclerenchymatous cortex with cortical appendages of *C. poroxyloides* (capitate glands). C.B. 1,221G bot #2 X 54(CP-B-2).

Fig. 25. Smaller cortical appendage of the type shown in Fig. 24. C.B. 5,821 top A #3 X 158 (CP-B-2).

Fig. 26. Transverse section of stem showing secretory cavity in pith, and primary vascular bundles at the margin of the secondary xylem. C.B. 132 A top #24 X 48(CP-D-5).

Fig. 27. Transverse stem section illustrating mesarch primary bundle. Note the disposition of the protoxylem and centrally located parenchymatous strand. C.B. 5,821 bot A #1 X 135 (CP-B-2).

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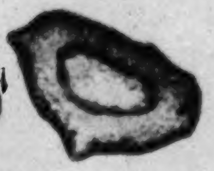

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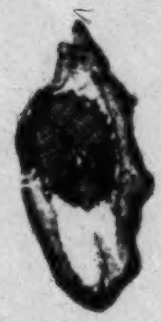

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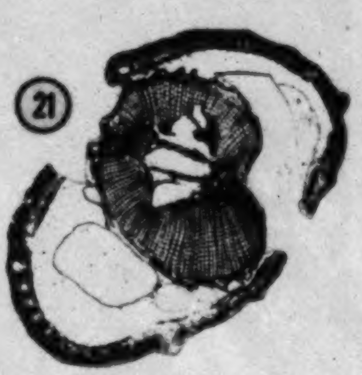

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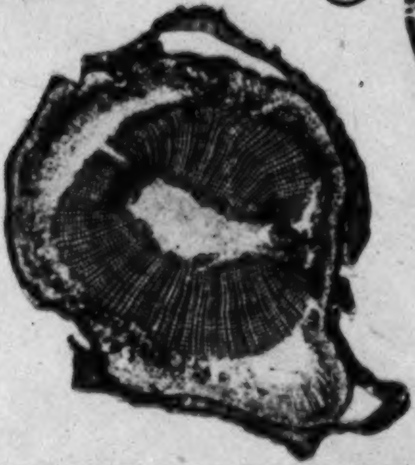

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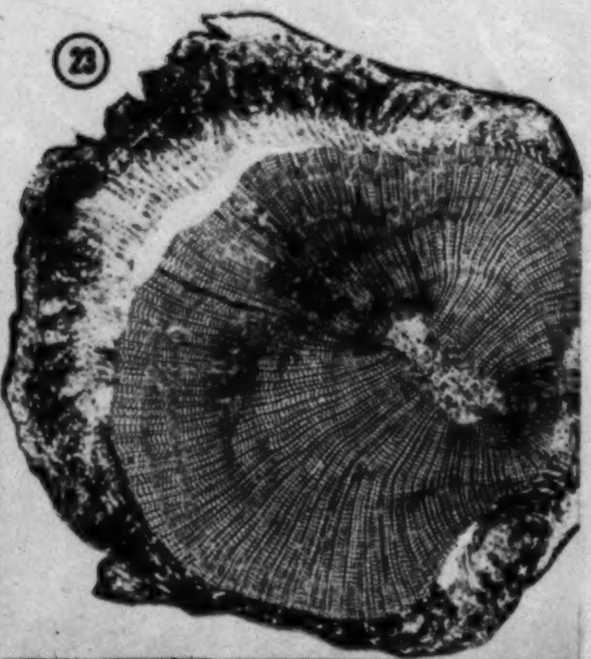

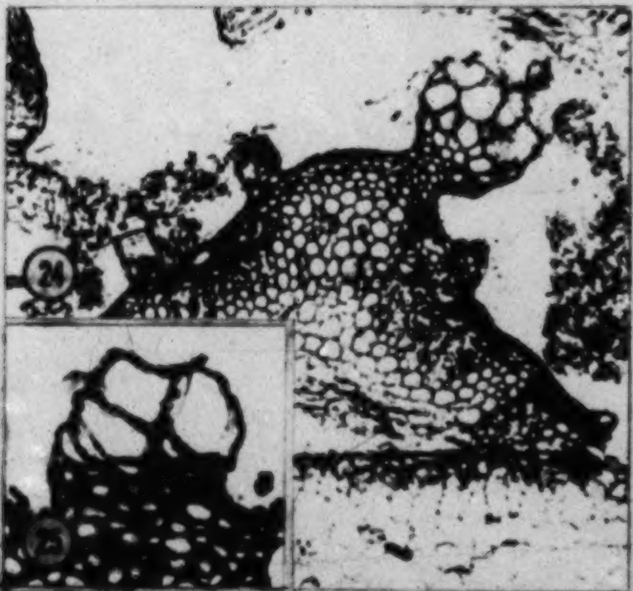

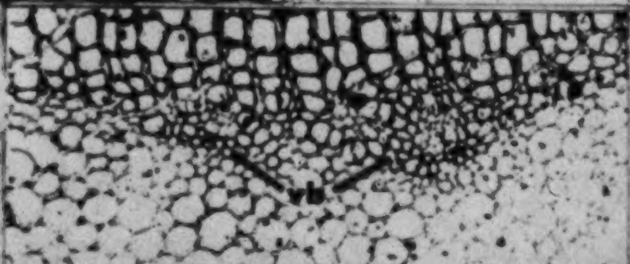

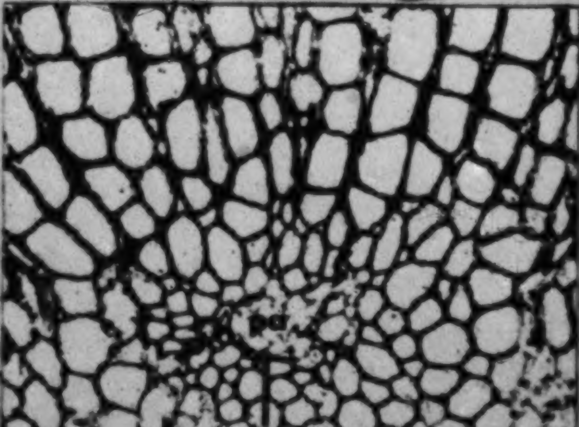

Figs. 28 - 35. *Callistophyton boyssetii*. (br=branch, bu=bud, l=leaf, r=root, s=stem.

Fig. 28 - 33. Transverse sections of stems representing a developmental sequence. Specimens previously described as *Calamopitys kansanum* (Fig. 30) and *Poroxylon* (Fig. 31,32) are included to illustrate that differences are due to unequal amounts of secondary development.

Fig. 28. C.B. 3,521C top a #2 X 6(CB-S-10)

Fig. 29. C.B. 5,754R top a #5 X 6(CB-S-11)

Fig. 30. #1,454 (CB-W-4)

Fig. 31. #1,431 X 6(CB-A-5)

Fig. 32. #1,421 X 6(CB-A-12)

Fig. 33. C.B. 3,987C bot #4 X 6(CB-S-13)

Fig. 34. Transverse section of specimen with large axillary branch and short internodes. Note that the stem and branch have not yet separated, and that the branch has produced a leaf and axillary bud. C.B. 3,521C top B #52 X 6(CB-S-9).

Fig. 35. Transverse section at nodal region showing petiole, axillary bud, and large branching root mass. C.B. 4,040K$_{(1)}$ bot #15 X 6 (CB-S-14).

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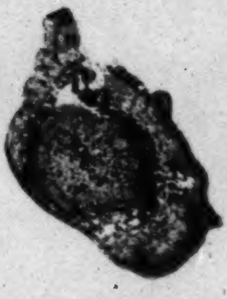

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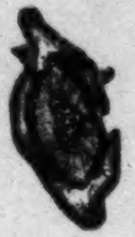

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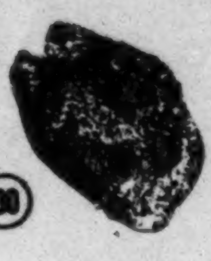

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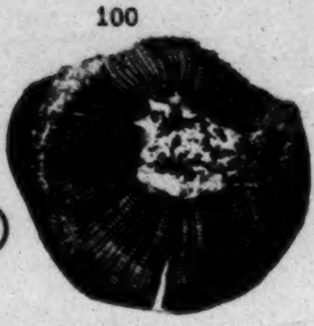

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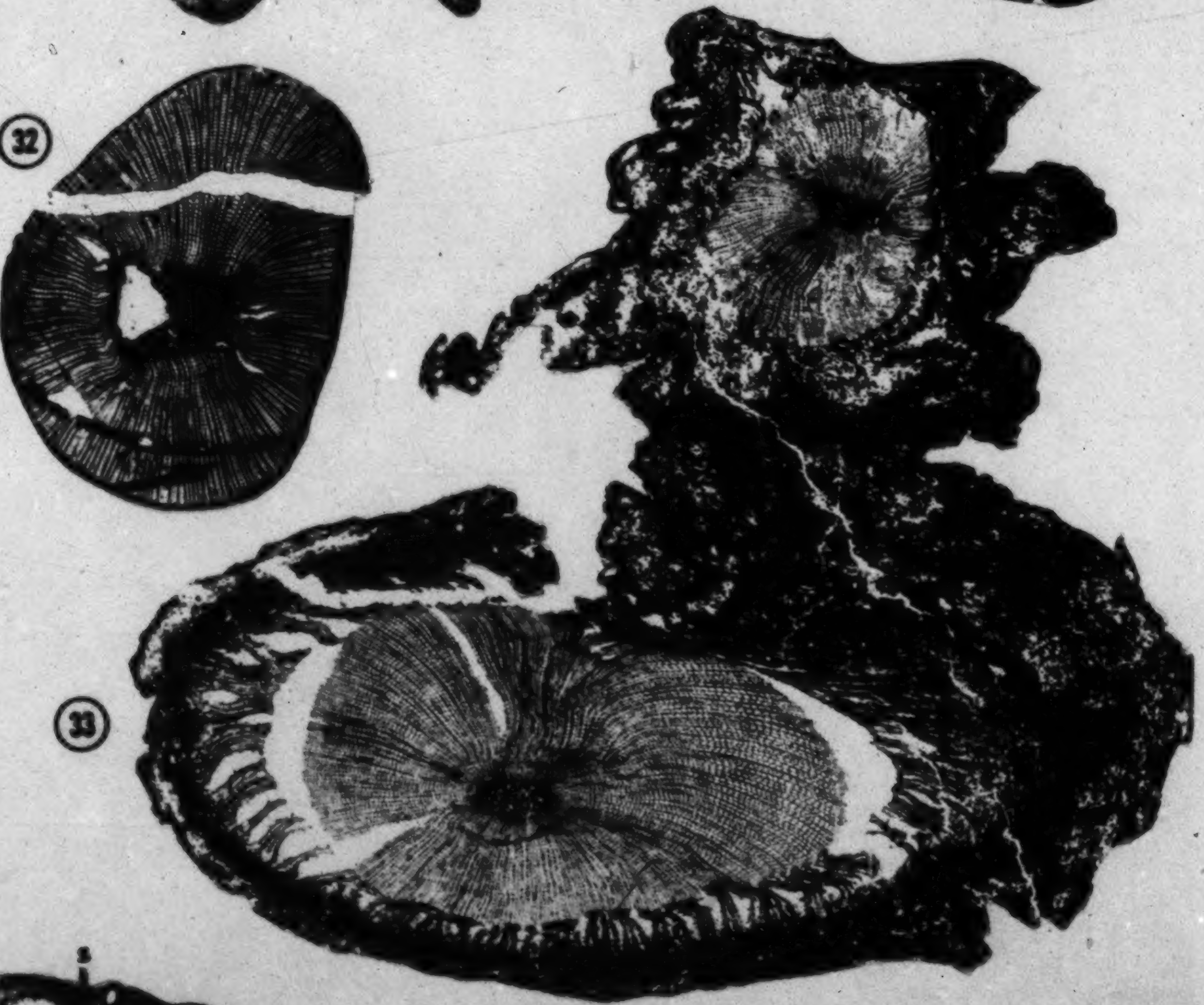

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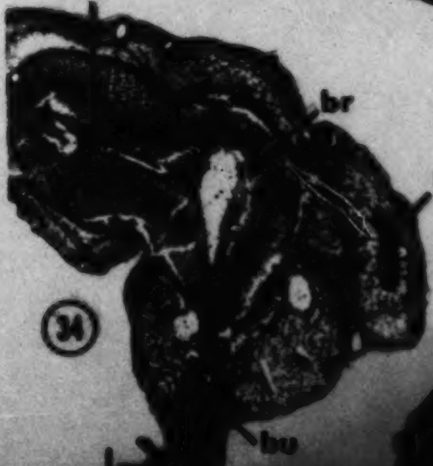

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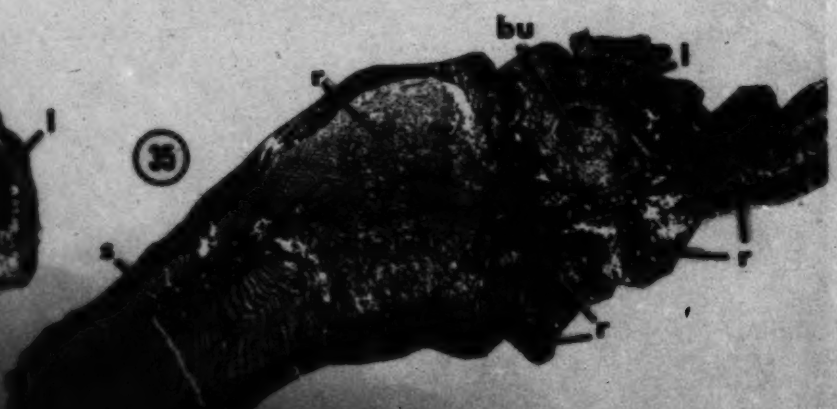


Figs. 36 - 43. *Callistophyton boyssetii.* (pa=parenchyma, pc=primary cortex, pd=periderm, pr=protoxylem, px=primary xylem, sc=secretory cavity, scl=sclerenchymatous cortex, sph=secondary phloem, sx=secondary xylem, vc=vascular cambium).

Fig. 36. Transverse section of sclerenchymatous cortex with secretory cavity and spine-like cortical appendage. C.B. 5,754N bot a #4 X 54(CB-S-11).

Fig. 37. Transverse section of dividing primary bundle. C.B. 5,754F top b #23 X 135(CB-S-2).

Fig. 38. Transverse section of primary bundle showing exarch structure. Note position of parenchyma strand and protoxylem. C.B. 5,754F top b #23 X 135 (CB-S-2).

Fig. 39. Transverse section of double leaf trace. Note the two protoxylem strands in each part of trace. #1,636(CB-A-5).

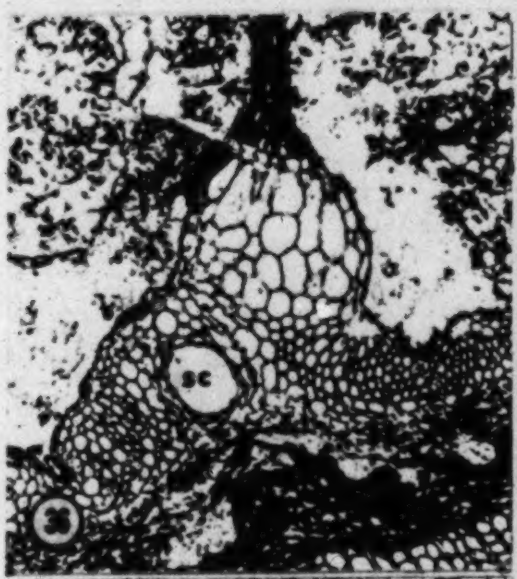
Fig. 40 - 43. Transverse sections of stems showing features at varying developmental stages. Fig. 40 shows first formed secondary tracheids and the position of phellogen differentiation (at arrows). Fig. 41 illustrates specimen with secondary phloem, periderm and separated sclerenchymatous cortex. In Fig. 42 sclerenchymatous cortex is absent, and in Fig. 43 thick-walled, sclereids are present in the secondary phloem, parenchymatous cortex and periderm.

Fig. 40. C.B. 3,259G bot #10 X 77(CB-S-1)

Fig. 41. C.B. 5,754I top b #13 X 86(CB-S-11)

Fig. 42. C.B. 5,754E top b #24 X 67(CB-S-2)

Fig. 43. C.B. 3,987D top #100 X 54(CB-S-13).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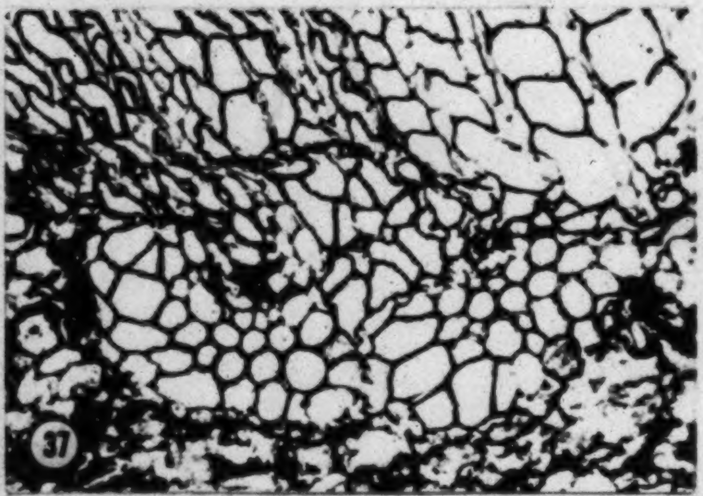
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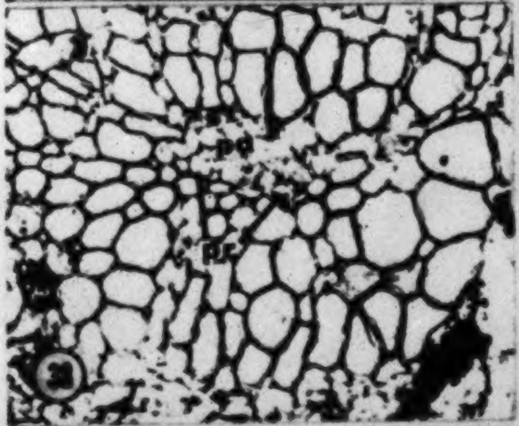
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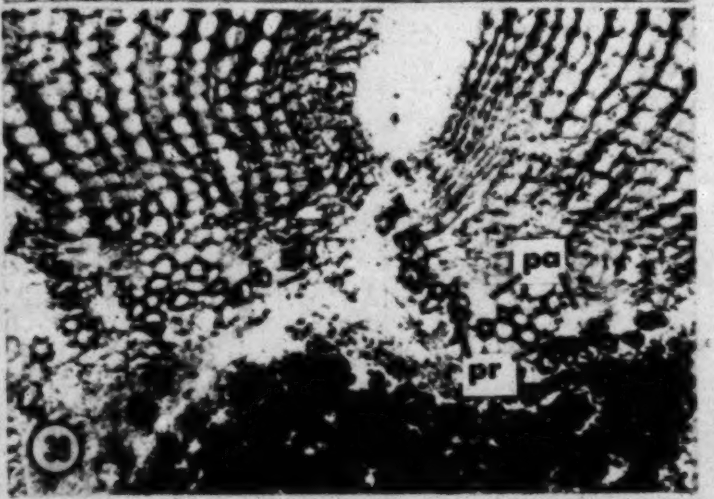
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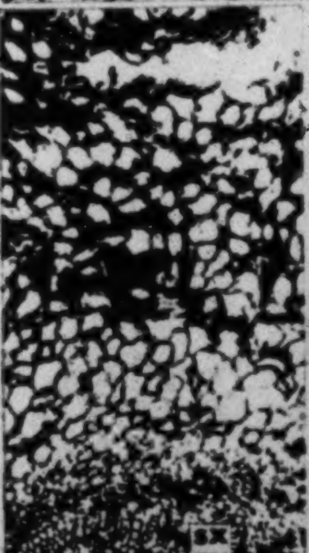
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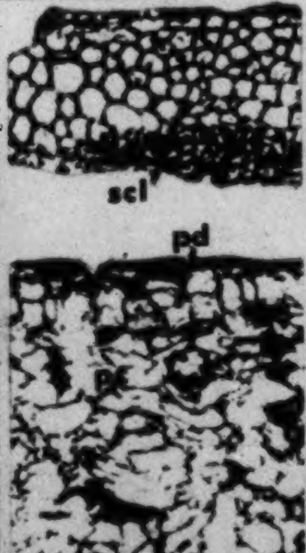
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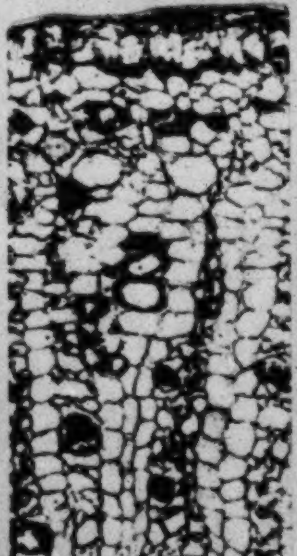
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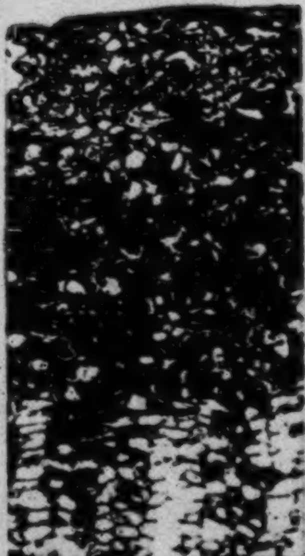
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Figs. 44 - 49. Transverse sections of stems showing disposition of primary xylem bundles. Figs. 44 - 47 at comparable levels to indicate similarity of specimens from different localities. Arrows indicate primary xylem bundles. Arrows with touching bases signify double stranded leaf traces.

Fig. 44. *Callistophyton poroxyloides*. C.B. 1,221H top #13 X 20(CP-B-2).

Fig. 45 - 49. *Callistophyton boyssetii*.

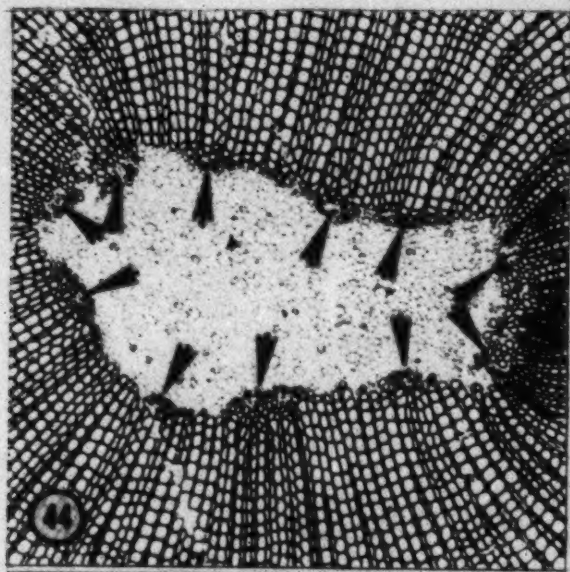
Fig. 45. (previously designated as *Poroxylon*) #1,636 X 20(CB-A-5).

Fig. 46. (previously designated as *Calamopitys kansanum*) #1,454 X 20(CB-W-4).

Fig. 47. C.B. 5,754F bot b #14 X 20(CB-S-2).

Fig. 48. Section slightly distal to Fig. 47. Small points indicate tracheids to the axillary bud and adventitious roots. Large arrows indicate bundles that divide to produce xylem to the axillary appendages. C.B. 5,754H bot b #25 X 20(CB-S-2).

Fig. 49. Section slightly distal to Fig. 48 at level of axillary bud divergence. Note the inconspicuous nature of the primary xylem bundles (arrows) at this level. C.B. 5,754I top b #21 X 20(CB-S-2).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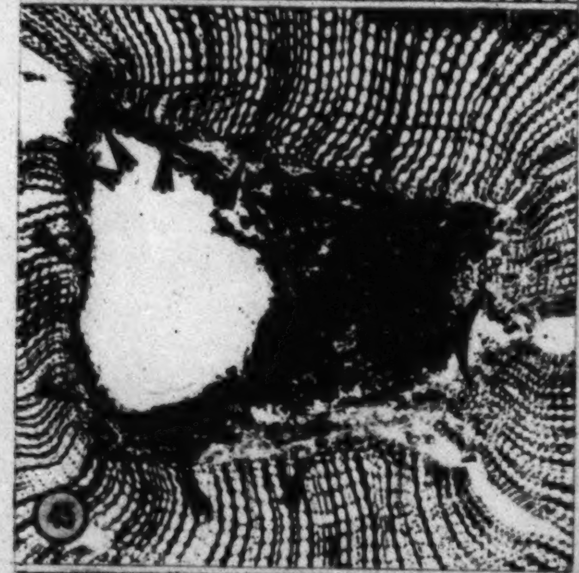
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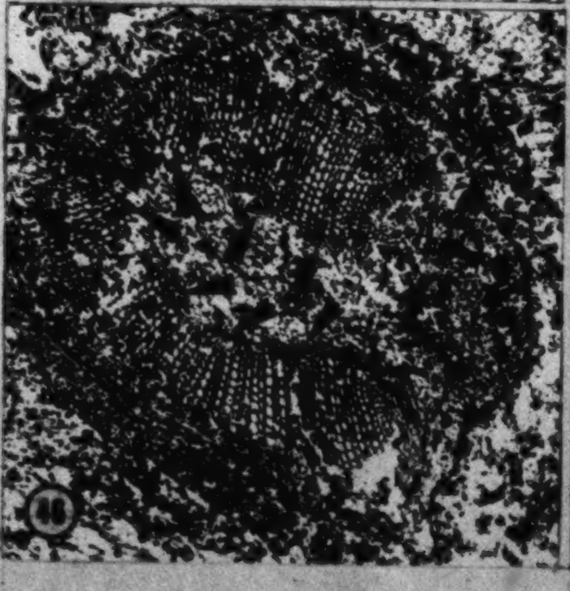
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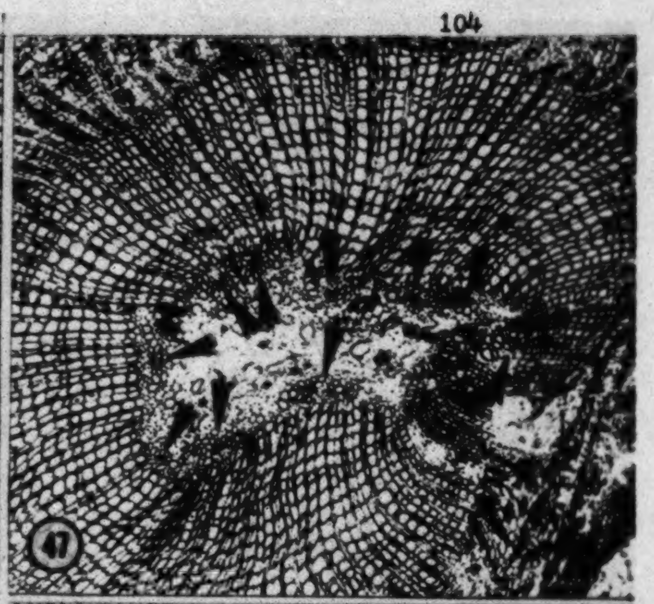
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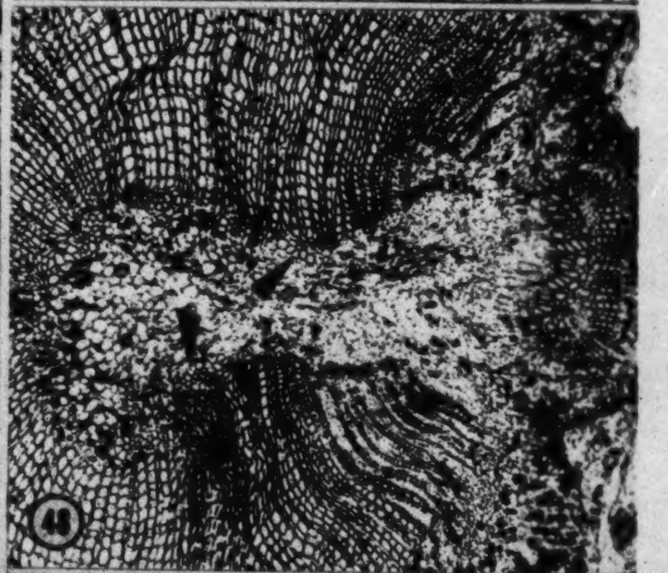
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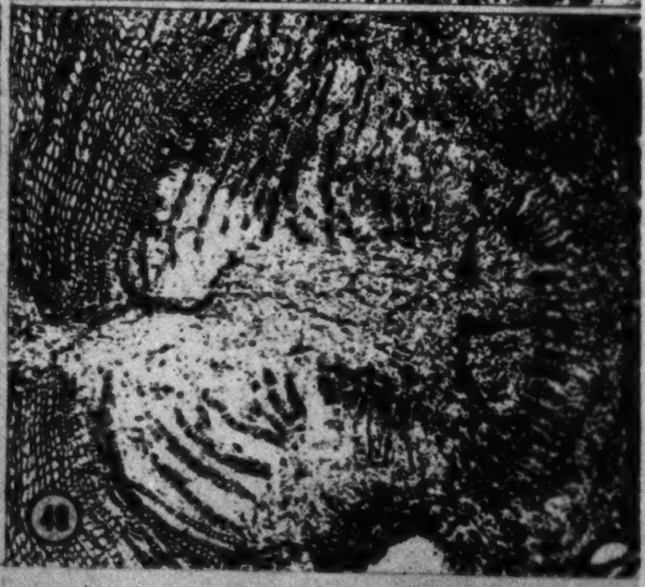
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Figs. 50 - 56. *Callistophyton poroxyloides.* Anatomical features of the stem. (ca=cambium, pa=phloem parenchyma, pe=periderm, ph=phloem, sc=sieve cell, x=xylem).

Fig. 50. Radial section of secondary wood. 1,221A$_{(2)}$ edge #3 X 54(CP-B-2).

Fig. 51. Transverse section of secondary xylem. C.B. 132 B bot #16 X 54(CP-B-1).

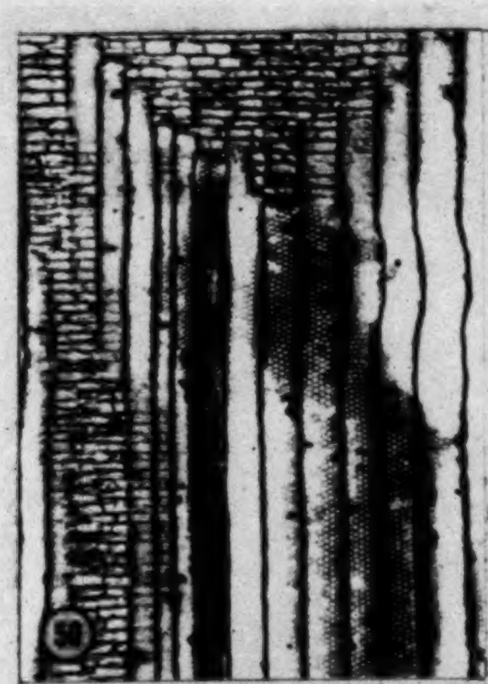
Fig. 52. Longitudinal section of primary xylem showing wall thickening patterns. C.B. 1,221a$_{(2)}$ edge #3 X 210(CP-B-2).

Fig. 53. Radial section of secondary phloem (at left) and periderm (at right). Note the resin canal-like structures in both zones. C.B. 1,221d$_{(1)}$ edge #5 X 54(CP-B-1).

Fig. 54. Radial section of secondary xylem showing pitting of tracheid (at right) and large, oblique, simple pits on ray parenchyma cells (at right). C.B. 1,221A$_{(2)}$ edge #3 X 210 (CP-B-1).

Fig. 55. Transverse section showing features of the secondary phloem, vascular cambium, and secondary xylem. C.B. 132 B bot #16 X 54 (CP-D-5).

Fig. 56. Tangential section of secondary xylem. C.B. 1,221D$_{(1)}$ edge #14 X 54(CP-B-2).



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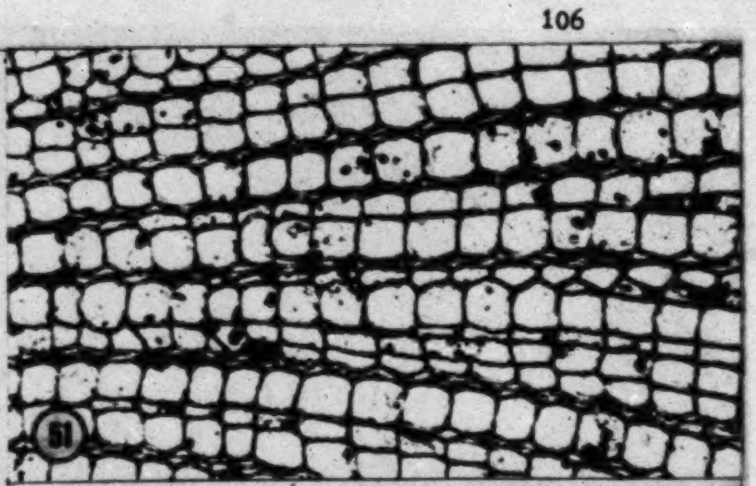

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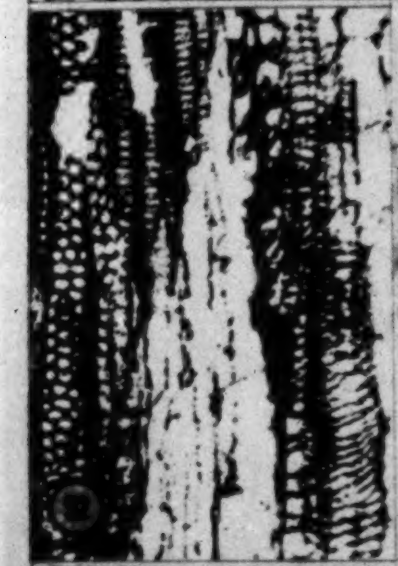

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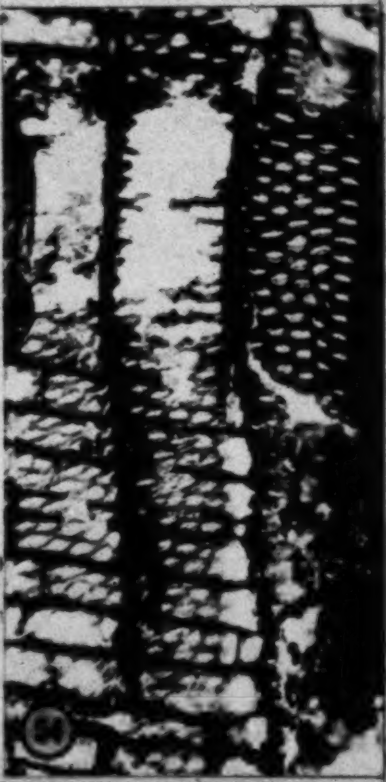

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Figs. 57 - 65. *Callistophyton boyssetii.* Anatomical features of stems from North American deposits. (ca=cambium, pa=phloem parenchyma, pe=periderm, ph=phloem, sc=sieve cell, x=xylem).

Fig. 57. Radial section of secondary xylem with pith at far left. C.B. 3,987C side #11 X 54 (CB-S-13).

Fig. 58. Transverse section of secondary xylem. C.B. 3,987C bot #47 X54(CB-S-13).

Fig. 59. Radial section of primary bundle; protoxylem at center and metaxylem at right. C.B. 3,554A side #43 X 420(CB-S-15).

Fig. 60. Tangential section of secondary xylem. C.B. 3,987C side #1 X 54(CB-S-13).

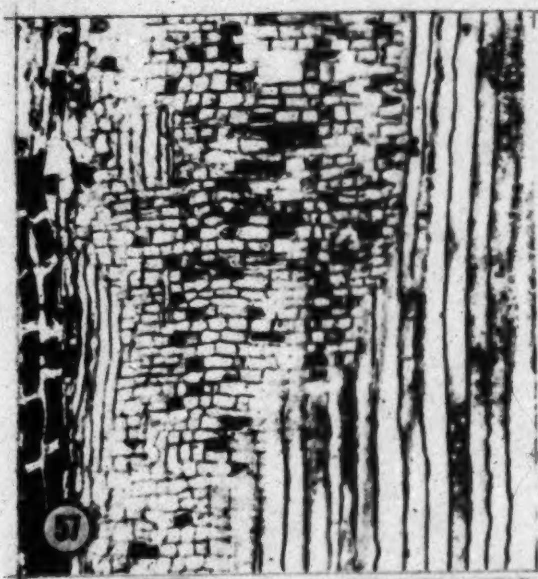
Fig. 61. Tangential section of secondary xylem in region immediately above an axillary bud. C.B. 4,123D top #78 X 54(CB-S-16).

Fig. 62. Radial section showing large, oblique, simple pits on ray parenchyma cell walls. C.B. 3,987C side #11 X 540(CB-S-13).

Fig. 63. Transverse section showing inner cortex (at top), secondary phloem, vascular cambium, and secondary xylem. C.B. 5,754E top b #24 X 67(CB-S-2).

Fig. 64. Radial section of secondary tracheids showing pitting pattern. Note crossed, slit-like apertures. C.B. 3,987C side #16 X 540 (CB-S-13).

Fig. 65. Radial section of secondary phloem (at left) and periderm (at right). C.B. 3,987C side #5 X 54(CB-S-13).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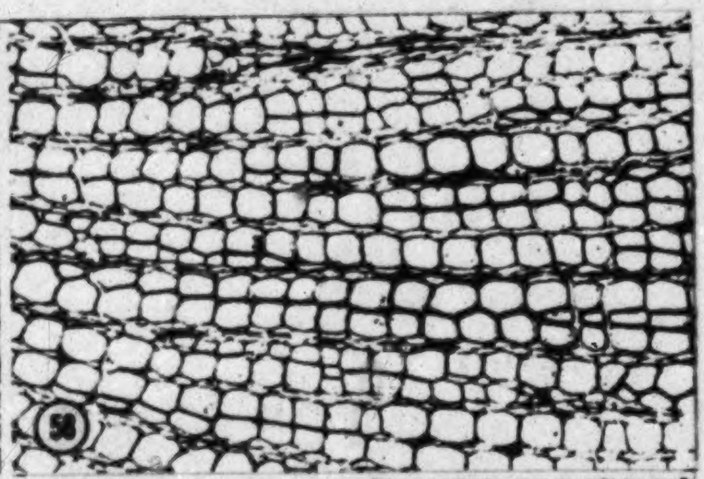
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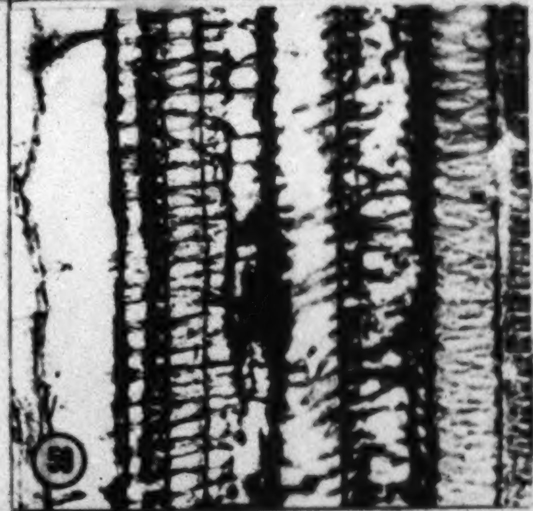
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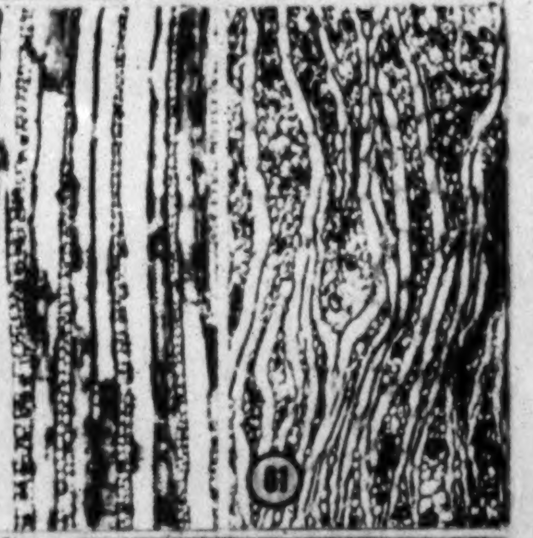
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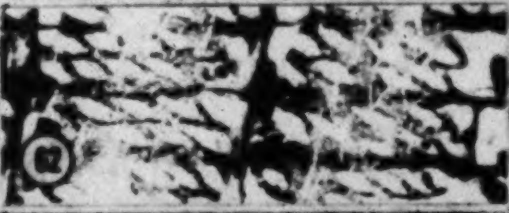
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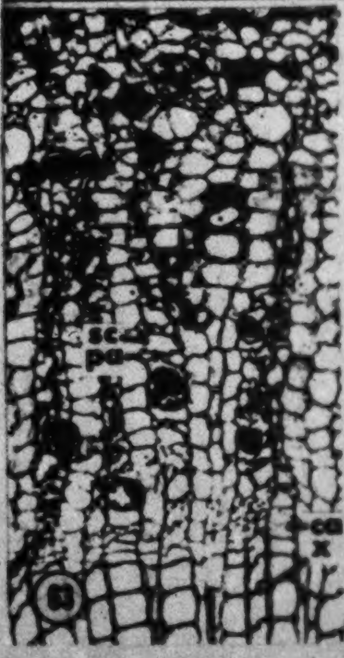
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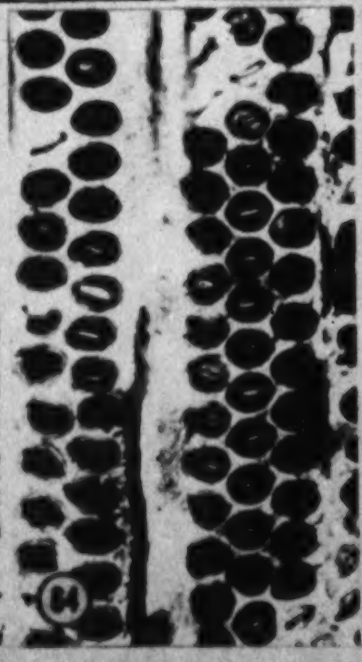
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Figs. 66 - 72. *Callistophyton boyssetii*. Anatomical features of stems from France (previously designated as *Poroxylon*) for comparison to those of the North American specimens. (pa=phloem parenchyma, pe=periderm, ph=phloem, sc=sieve cells).

Fig. 66. Radial section of secondary xylem. Compare with Fig. 50, 57. #2,965 X 54(CB-A-17).

Fig. 67. Transverse section of secondary xylem. Compare with Fig. 51, 58. #1,636 X 54(CB-A-5).

Fig. 68. Longitudinal section of primary bundle. Compare to Fig. 52, 59. #1,432 X 400(CB-A-18).

Fig. 69. Tangential section of secondary xylem. Compare with Fig. 56, 60. #1,423 X 100(CB-A-19).

Fig. 70. Radial section of secondary wood. Note that poorly preserved pits appear as hexagonal meshwork. Compare with Fig. 54, 64. #2,965 (CB-A-17).

Fig. 71. Cross section of secondary phloem. Compare disposition of cells with Fig. 55, 63. #2,964(CB-A-7).

Fig. 72. Radial section of secondary phloem (at left) and periderm (at right). Compare with Fig. 65. #2,965 X 54(CB-A-17).

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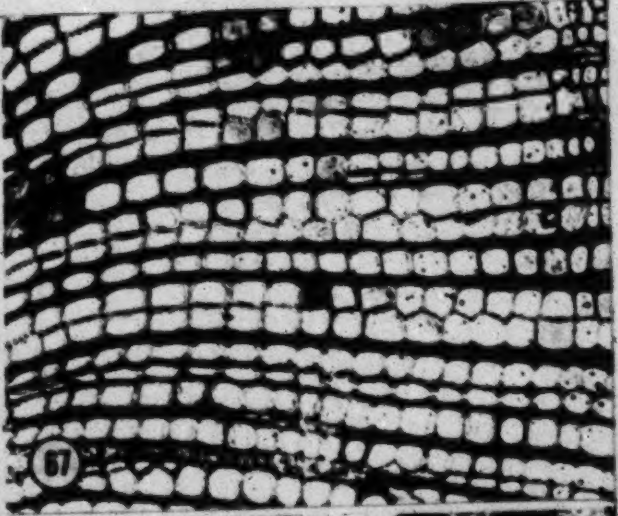
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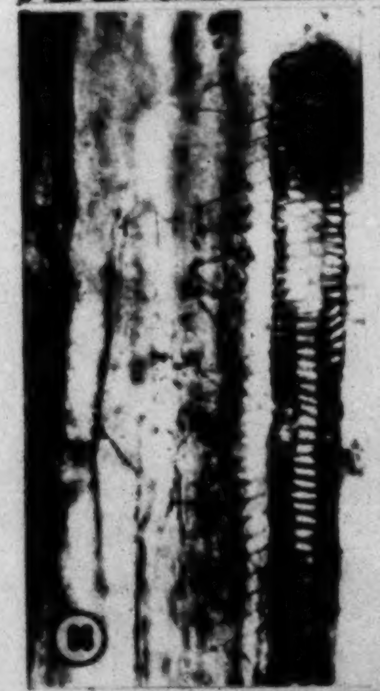
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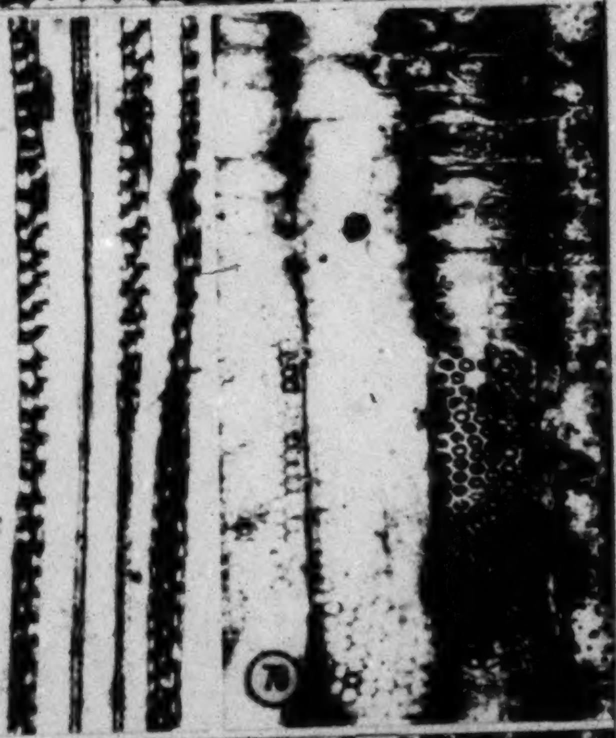
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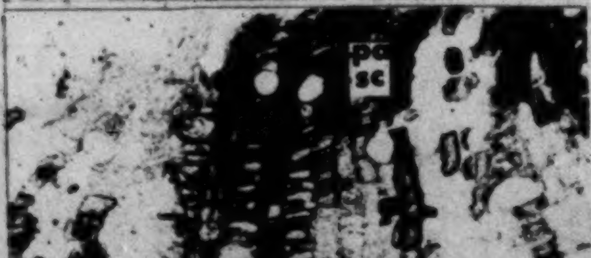

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Figs. 73 - 83. *Callistophyton* foliage. Fig. 75, 77 and 81 = *C. poroxyloides*. Fig. 73, 74, 76, 79, 80, 82 and 83 = *C. boyssetii*. (hb=hair base, ph=phloem, s=sclerenchyma, sc=secretory cavity, t=trace, vb=vascular bundle).

Fig. 73. Transverse section near base of small petiole. C.B. 908E top #26 X 12(CB-S-20).

Fig. 74. Transverse section near base of large petiole. Compare to Fig. 73. C.B. 3,963B top #31 X 12(CB-S-21).

Fig. 75. Section view of pinnule with lamina attached to one side of midvein, and homogeneous, tightly-packed mesophyll. C.B. 5,821 top b #12 X 27(CP-B-10).

Fig. 76. Petiole near the point of dichotomy. Note two equal sized traces and dividing cortex. C.B. 908B bot #105 X 12(CB-S-22).

Fig. 77. Section view of pinnule lamina in the area of a vein. Note the secretory cavity and palisade mesophyll (at arrow). C.B. 5,821B top #15 X 42(CP-B-10).

Fig. 78. Transverse section of pinnule showing lamina attached to both sides of midvein. C.B. 908C top f #22 X 12(CB-S-23).

Fig. 79. Pinnule lamina with spaces between mesophyll cells and well preserved epidermis. C.B. 2,746D$_{(1)}$ side #17 X 100(CB-W-24).

Fig. 80. Pinnule lamina with tightly packed, homogeneous mesophyll. Note dark cells around veins. C.B. 5,754A bot f #10 X 103(CB-S-25).

Fig. 81. Broken pieces of pinnule with sclerenchyma ad- and abaxial to the veins, and spaces between mesophyll cells. C.B. 4,127F bot #113 X 42(CP-B-11).

Fig. 82. Leaf trace bundles in cortex of stem. Note phloem on abaxial surface only. C.B. 5,754M bot p #141 X 54(CB-S-26).

Fig. 83. Transverse section of petiole with primary pinnae trace diverging at left. C.B. 908E top #46 X 54(CB-S-20).

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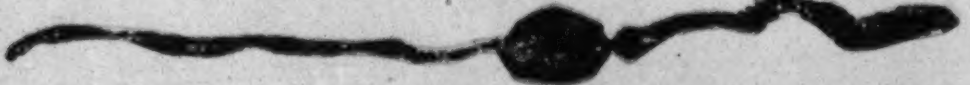
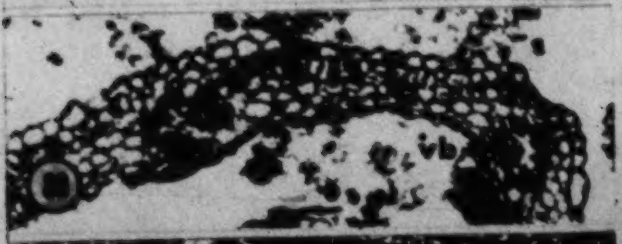
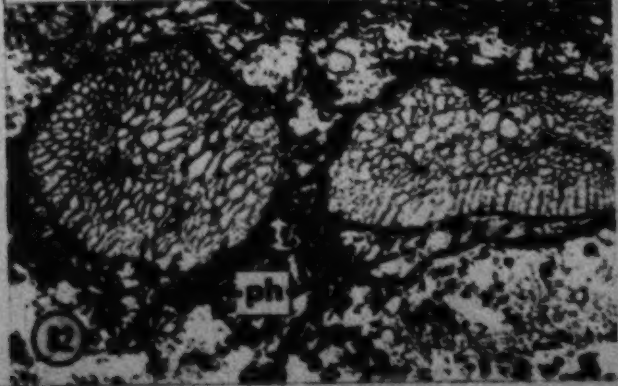
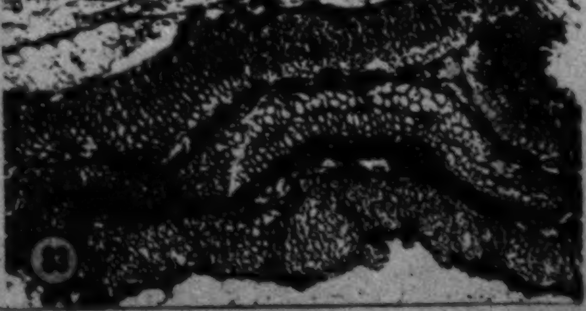








Figs. 84 - 89. *Callistophyton boyssetii* foliage. (e=epidermis, pp=primary pinnae, r=rachis, sc=secretory cavity, sp=secondary pinnae).

Fig. 84. Isolated crosier showing several orders of pinnae. Note glandular cavities. C.B. 327E top #11 X 12(CB-S-27).

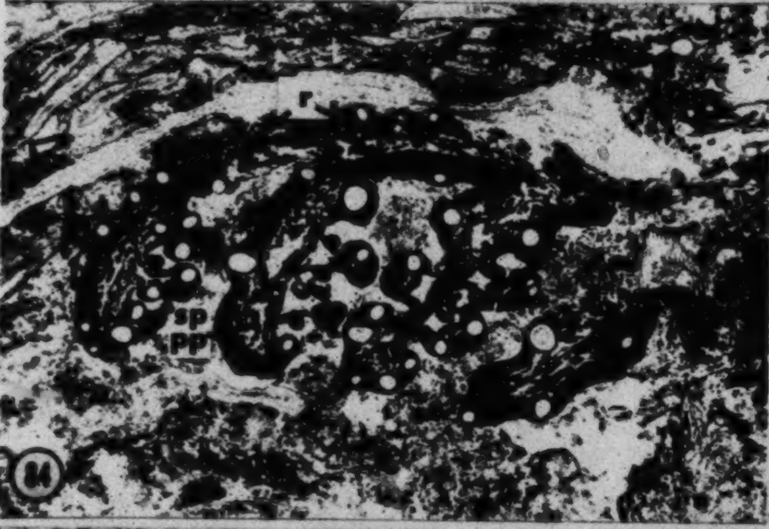
Fig. 85. Paradermal section of pinnule fragment. Note lobed margin, at right. C.B. 2,746D$_{(1)}$ side #18 X 13(CB-W-24).

Fig. 86. Paradermal section of pinnule fragment showing venation features. Lateral diverges from midvein (at arrow) and dichotomizes 4 times toward margin. C.B. 2,746D$_{(1)}$ side #31 X 18(CB-W-24).

Fig. 87. Paradermal section of pinnule with tightly packed, homogeneous mesophyll parenchyma. C.B. 5,754A bot f #12 X 103(CB-S-25).

Fig. 88. Paradermal section of pinnule fragment with tightly packed mesophyll near the adaxial surface, and weakly developed plates of mesophyll (at arrow) separated by lacunae toward abaxial surface. C.B. 2,746D$_{(1)}$ side #26 X 54(CB-W-24).

Fig. 89. Surface view of pinnule epidermis. Note the arrangement of cells opposite veins, and the random orientation of cells between the veins. C.B. 2,746D$_{(1)}$ side #31 X 170(CB- W-24).



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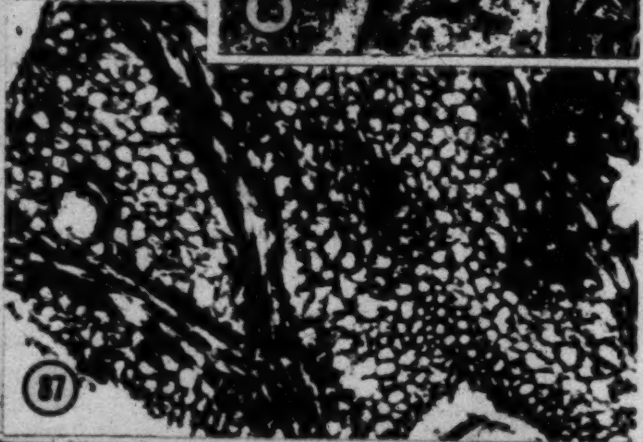

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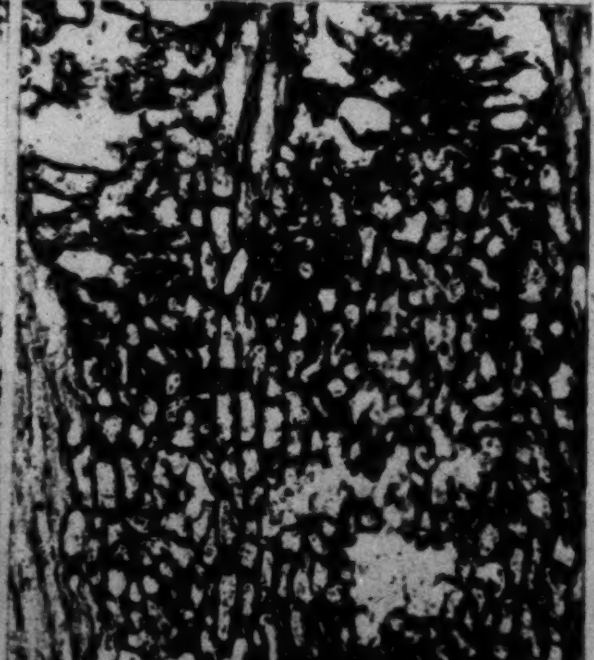

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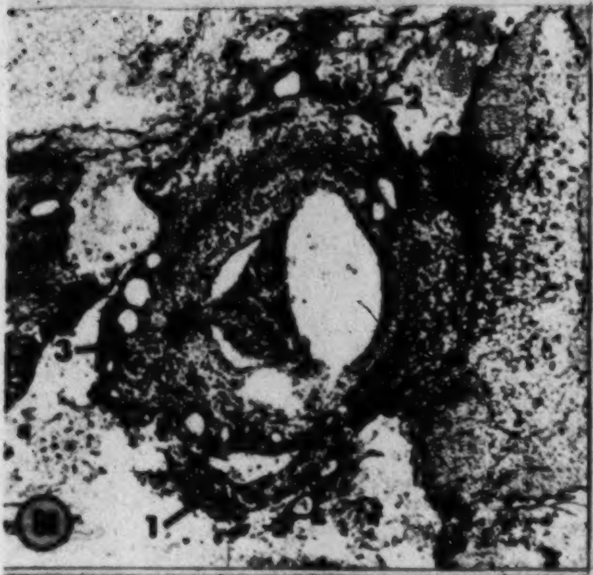
Figs. 90 - 95. *Callistophyton boyssetii*. Serial transverse sections from near the base (Fig. 90) to above the apical meristem (Fig. 95) of an axillary bud. The leaves are numbered in the order of their divergence (from bottom to top). Note that leaves 1 - 5 are entire margined and envelope the bud, while leaf 6 shows evidence of primary pinnae (Fig. 93 at arrows).

Figures 90 - 95. C.B. 3,259G bot, #138, #123, #99, #96, #82, and #74 respectively.

All Figs. X 16(CB-S-1).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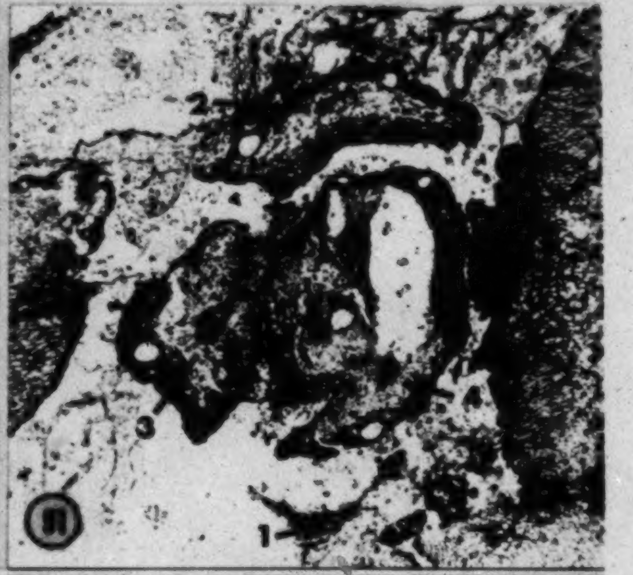
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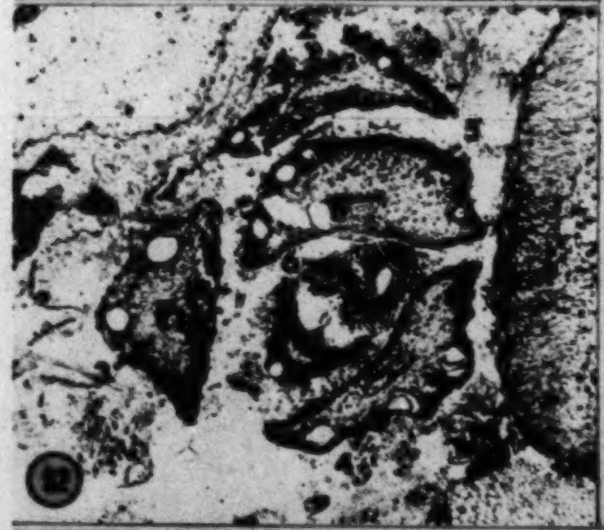
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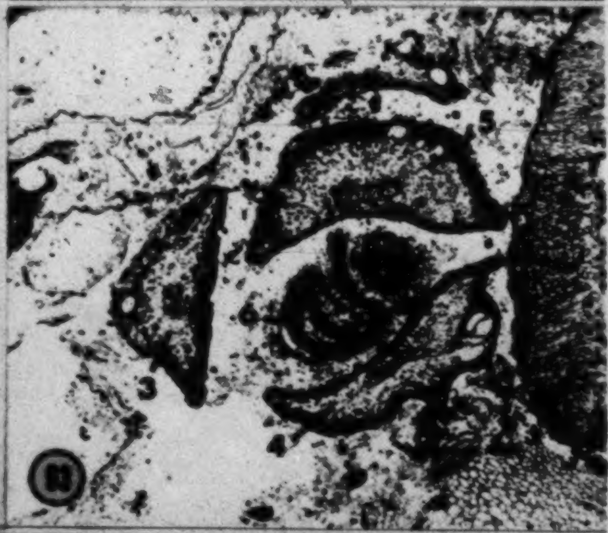
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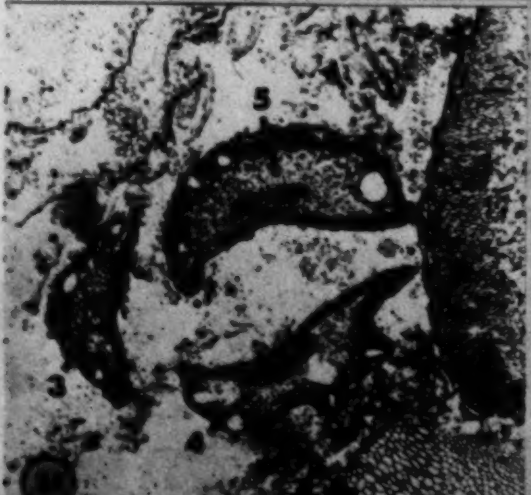
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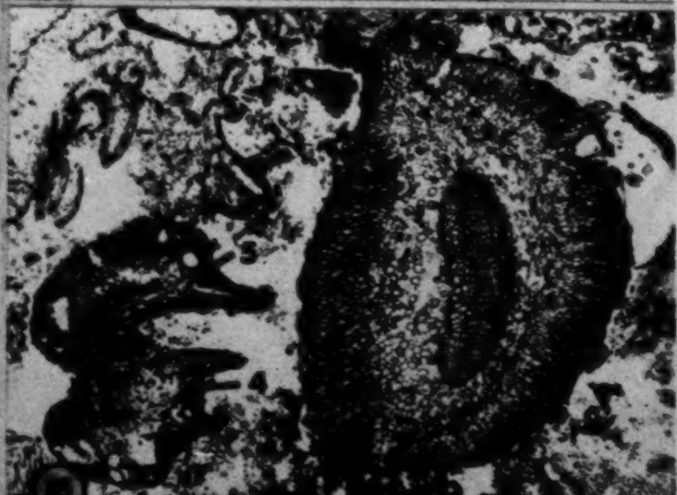
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Figs. 96 - 104. *Callistophyton poroxyloides.* Stem apex with immature leaves. (b=bud, l=leaf, mh=multicellular hairs, pp=primary pinnae, px=protoxylem, r=rachis, sp=secondary pinnae).

Fig. 96 - 101. Serial sections from below apical bud (Fig. 96) to level above apical meristem (Fig. 101). Note the divergence of five petiole bases, and dense covering of multicellular hairs. Compare immature leaf in Fig. 100-101 with isolated crosier in Fig. 84.

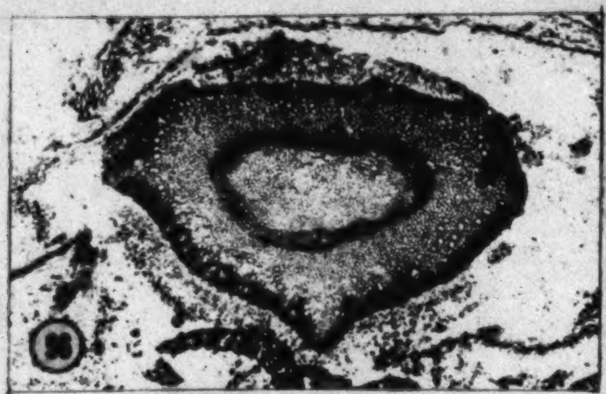
Fig. 96 - 101 = #1,689, #1,699, #1,700, #1,694, #1,691, #1,690 respectively.

All Figs. X 12(CP-B-6).

Fig. 102. Transverse section at level of Fig. 96. Note protoxylem tracheids among procambial cells. #1,687 X 48(CP-B-6).

Fig. 103. Bud present in axil of leaf at left of Fig. 98. First scale-like leaf has diverged at left. #1,699 X 33(CP-B-6).

Fig. 104. Scale-like leaves distal to apical meristem of bud in Fig. 103. #1,698(CP-B-6).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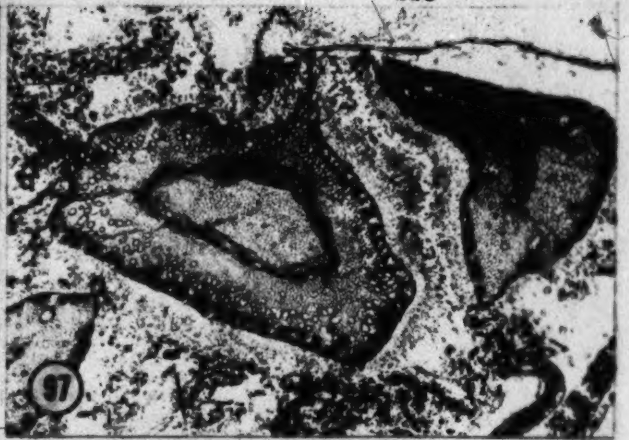
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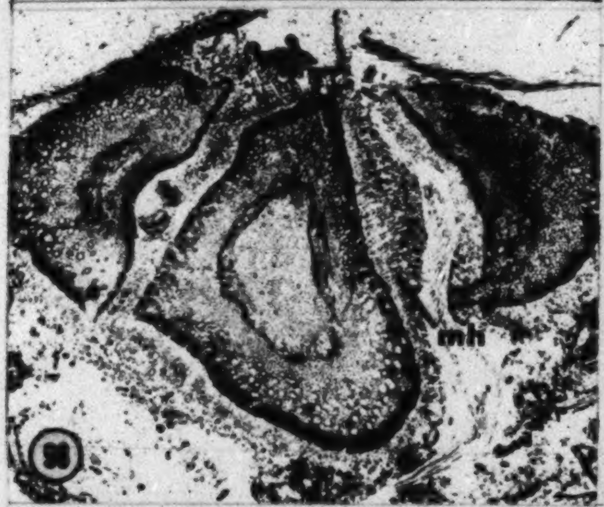
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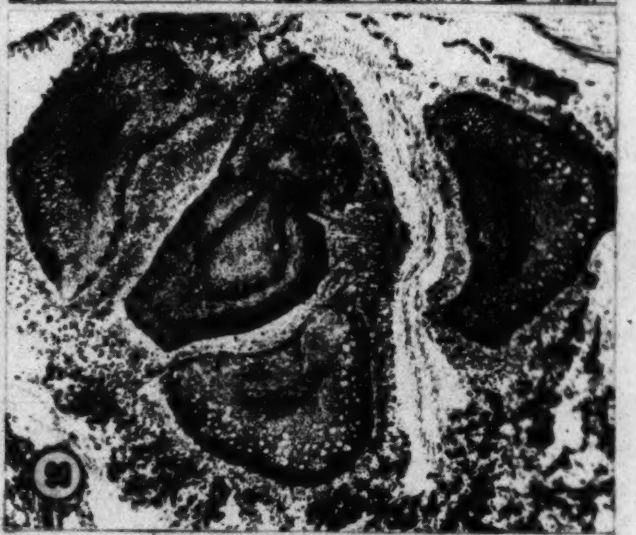
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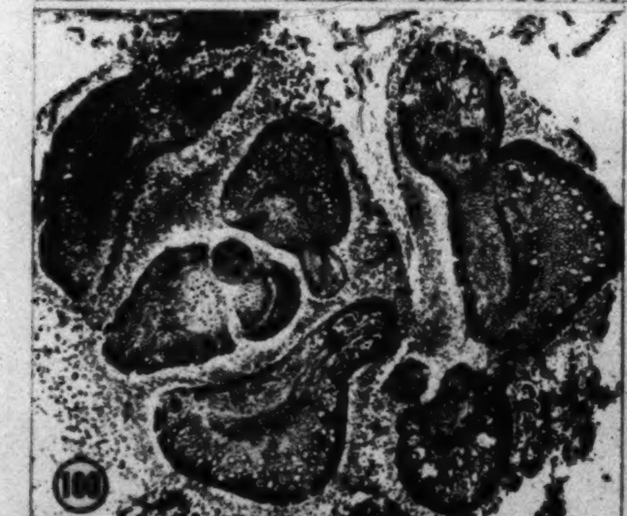
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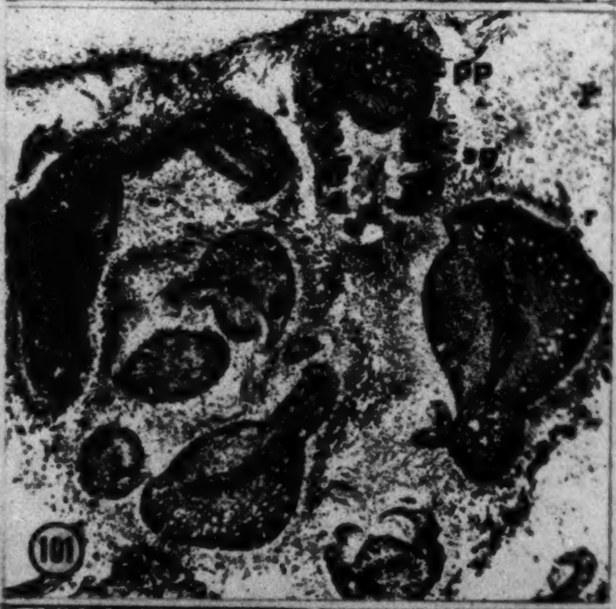
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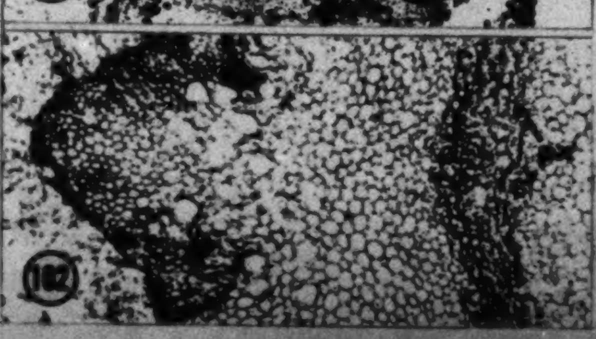
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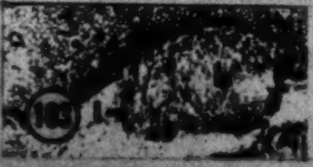
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Figs. 105 - 111. *Callistophyton boyssetii.* (b=bud, lt=leaf trace, r=root, rt=root trace, s=stem).

Fig. 105. Longitudinal section of nodal region showing the relative positions of the leaf trace, bud, and roots. Note that the leaf trace terminates in the stem cortex indicating earlier loss of the leaf. C.B. 2,380A bot #4 X 10(CB-S-28).

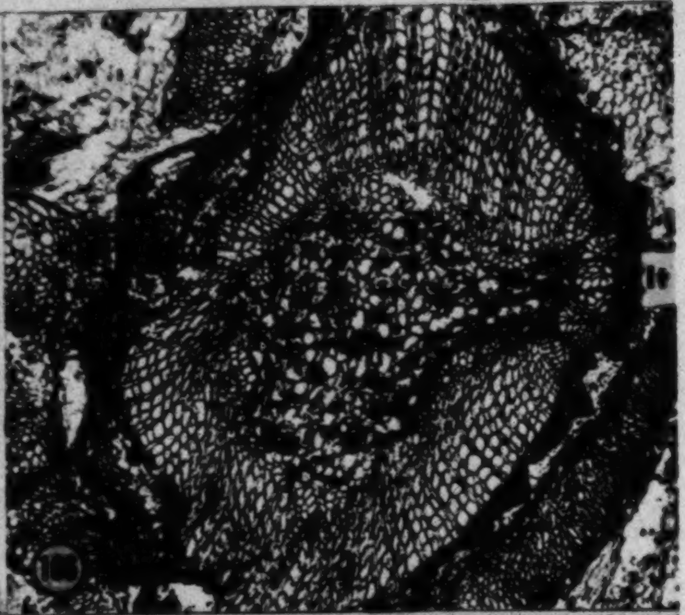
Fig. 106 - 109. Transverse sections through nodal region showing (106) divergence of leaf trace from stele, (107) leaf trace and axillary bud trace, (108) divergence of root trace xylem, and (109) diverging root trace and diverging roots.

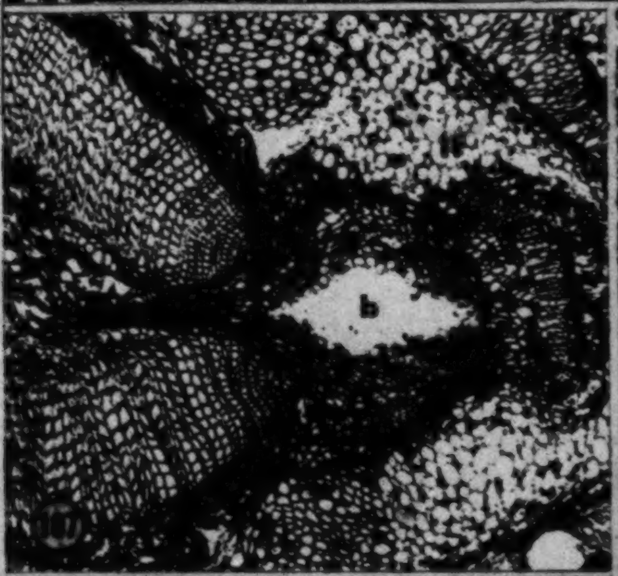
Fig. 106 - 109 = C.B. 5,754S top #6,$R_{(1)}$ bot #58, $R_{(1)}$ top #59, $R_{(1)}$ top #44 respectively.

All Figs. X 40(CB- S-10).

Fig. 110. Transverse section of roots. Arrow indicates lateral root origin at protoxylem strand. C.B. 289 A bot #75 X 11(CB- S-29).

Fig. 111. Transverse section of small and relatively immature roots. Arrow indicates position of epidermis. C.B. 5,743$G_{(1)}$ top b #2 X 30(CB-S-30).

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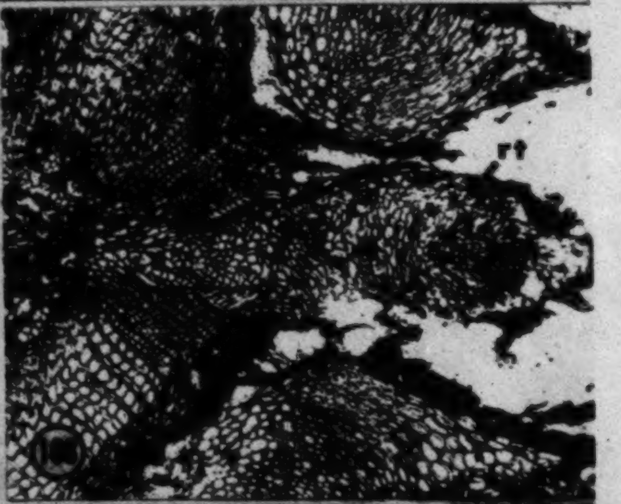
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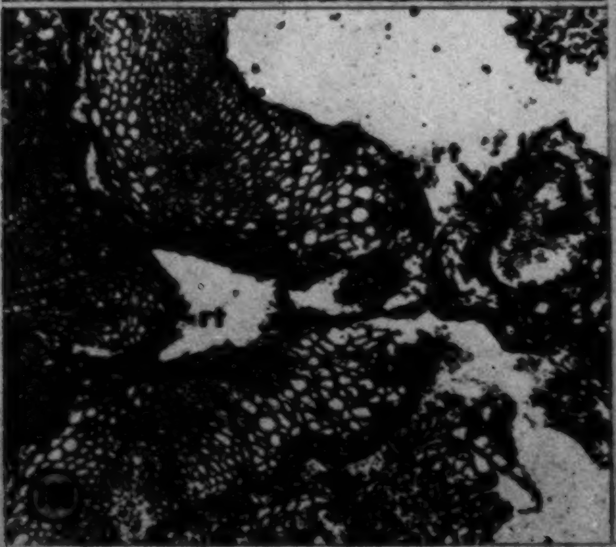
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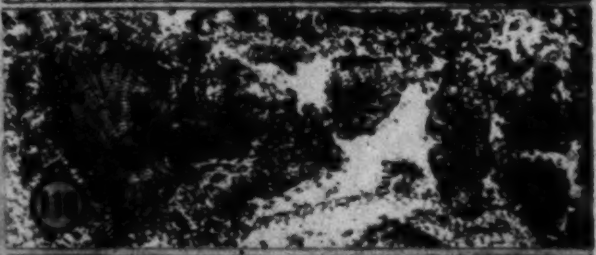
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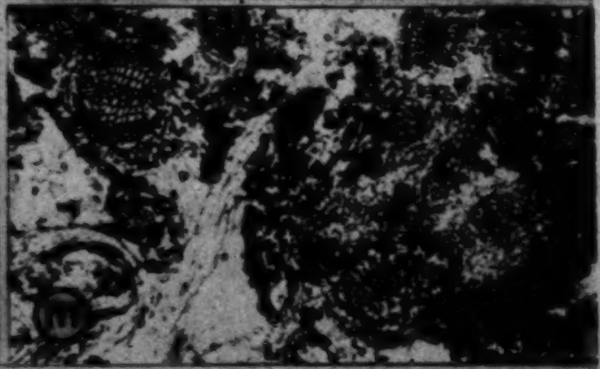
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